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Early Triassic Recovery from the end-Permian Mass Extinction of Benthic Ecosystems in the Palaeotropics

Dissertation

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Dedicated to my wife Peggy, and our children Yannek & Maja.

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Abstract

The end-Permian mass extinction is widely accepted to have been the greatest biotic crises in the history of meatzoan life. The understanding of the subsequent recovery during the Early Triassic is of utmost importance to address fundamental question in earth system science: (i) how do ecosystems respond to large-scale environmental stress, (ii) how quickly do ecosystems recover, and (iii) how do evolutionary processes operate under the unusual conditions of vacated ecospace?

The first studies on Early Triassic communities suggested that no significant recovery took place during the entire stage with an approximate duration of 5 million years. It has been proposed that this pattern was caused by persistent environmental stress which delayed ecological and taxonomic recovery. However, this notion rests on data with limited taxonomic, stratigraphic, and environmental resolution. Furthemore, with the exception of some early studies, proposed models to explain the recovery pattern were exclusively based on extrinsic (abiotic) controlling factors whereas macro-ecological consequences of the extinction itself were largely ignored.

The aim of the presented thesis is to reconstruct a detailed picture of the benthic recovery at the eastern and western tropical shelf of Pangaea. We use quantitative palaeoecological analysis of selected successions in the Western U.S. and the Dolomites to distinguish between local and global signals. The analysis of different depositional settings (e.g. deep vs. shallow shelf) should elucidate whether recovery was restricted to certain environments. Another central aspect of this thesis is to revisit the role of intrinsic controlling factors on the recovery.

A first significant finding is that benthic ecosystem show a unexpectedly early global recovery signal during the upper Griesbachian, only some 0.5 Million years after the extinction. This questions the influence or the spatial and temporal extent of stress factors such as shallow marine anoxia. The data from the succeeding Dienerian time interval show that benthic ecosystem declined at least on an interregional scale approximately 1 million years after the extinction. The next and most significant recovery signal is observed in lower Spathian strata. During this time interval, 2 Million years after the extinction, many benthic organisms that dominated Mesozoic ecosystems such as bivalves, gastropods, porifers, echinoderms and articulated brachiopods became established in relatively diverse communities and represent the rootstock of the subsequent radiation. The comparison of both regions also shows that local stress factors may influence the overall recovery signal. The overall signal however, suggests that instead of persisting, repeated but short environmental perturbations contributed to the delayed recovery.

The second aspect advanced by this thesis is the reconsideration of intrinsic factors on the recovery patterns. The analysis of the Virgin Formation of southwestern Utah has shown that many subhabitats were inhabitat by many generalistic species. Such traits were also traditionally interpreted to reflect environmental stress. This is, however, at variance with the finding that these communities were comparatively complex and diverse. Alternatively, we propose that the low number of specialised benthic organisms reflects a generally low rate of competition within these habitats. The aftermaths of large mass extinctions are typically characterised by a low habitat (alpha) diversity, which would imply a low rate of niche overlap and thus low rate of competition within ecosystems. Such conditions would allow species to thrive outside their ecological optima. This should be reflected in a low between habitat (beta) diversity. Accordingly, after a sufficiently severe mass extinction event, beta diversity should rise when alpha diversity reaches a level which drives ecosystems into a mode allowing for competitive exclusion. This evolutionary principle should than cause species' to find "their" ecological optima along environmental gradients. A conclusive test of this model for Lower Triassic strata of the western U.S. confirms at least one prediction of this model: Whereas alpha diversity rises successively throughout the Early Triassic, beta diversity remained constantly low. If this model is correct, it could explain why the actual radiation of many benthic clades lags behind the definite onset of recovery. Future studies which will consider Middle Triassic and Permian ecosystems will help to test the validity of this model. The general low biodiversity especially during the earliest Triassic has usually been interpreted to reflect environmental stress. In this thesis, it is argued that the general usability of the relationship between low diversity and hostile conditions was at least diminished in the aftermath of the mass extinction which per definition reduces diversity in the first place.

This thesis represents a significant advance in the understanding and reconstruction of ecosystem in the aftermath of the greatest mass extinction recorded in the Phanerozoic. The observed data a best explained by (i) short phased of environmental stress and (ii) the nonactualistic ecology which was a direct consequence of the dramatic loss in biodiversity and collapse of marine ecosystems.

key words: recovery • benthos • evolution • mass extinction •Early Triassic • bivalves • palaeoecology

Kurzfassung

Die Krise am Ende des Perms stellt das größte Massenaussterben in der Geschichte der Metazoen dar. Das Verständnis über den Ablauf der sich anschließenden Erholungsphase während der Untertrias ist von großer Bedeutung für wichtige Fragen der Geo- und Biowissenschaften. Wie reagieren Ökosysteme auf globale Umweltveränderungen? Wie schnell können sie sich davon erholen? Erlauben die besonderen Bedingungen nach einem solchen Aussterben (geringe Biodiversität, Aufgabe und Neubesetzung ökologischer Nischen) einen besseren Blick auf prinzipielle Evolutionsprozesse?

Die ersten Analysen untertriassischer Faunengemeinschaften legten den Schluss nahe, dass während der ersten fünf Millionen Jahre keine nennenswerte Erholung stattgefunden hat. Dies wurde damit erklärt, dass während der Untertrias lang anhaltend schlechte Umweltbedingen die Radiation überlebender Tiergruppen verzögerte. Diese Interpretation stützt sich jedoch auf Daten mit geringer taxonomischer, stratigraphischer und räumlicher Auflösung. Bis auf wenige frühe Arbeiten greifen Erklärungsmodelle ausschließlich auf extrinsische Kontrollfaktoren (schlechte Umweltbedingungen) zurück, ohne die makroökologischen Konsequenzen eines solchen Aussterbeereignisses überhaupt in Betracht zu ziehen.

Das Ziel der vorliegenden Dissertation ist es, mit Hilfe von quantitativer Paläoökosystemanalyse ein möglichst genaues Bild der Erholungsmuster von benthischen Ökosystemen innerhalb der Paläotropen des westlichen und östlichen Schelfrandes von Pangäa zu rekonstruieren. Der Vergleich beider Lokalitäten (Südwesten der U.S.A. vs. Dolomiten) soll es erlauben, lokale von globalen Trends zu unterscheiden. Die differentielle Analyse verschiedener Ablagerungsbereiche (z.B. Tief- vs. Flachschelf) soll klären, ob Erholungsmuster an bestimmte Habitate gebunden waren. Ein zentrales Anliegen dieser Arbeit ist es, die Rolle von intrinsischen Mechanismen (z.B. intraspezifische und ökologische Wechselwirkungen) in Erklärungsmodelle der Erholung mit einzubeziehen.

Das erste wichtige Ergebnis ist die Dokumentation eines globalen Erholungssignals etwa 0.5 Millionen Jahre (während des oberen Griesbachiums) nach dem Massenaussterben. Permanente Stressfaktoren (Sauerstoffmangel in den Ozeanen) hatten demnach entweder kaum Einfluss auf die Erholung oder ihre geographische und zeitliche Ausdehnung war kleiner als bisher angenommen. Die Daten zeigen weiterhin, dass benthische Ökosysteme einen mindestens überregionalen Einbruch erlebten, der durch eher kurzlebige Stressfaktoren ca. 1 Millionen Jahre (im oberen Dienerium) nach dem Aussterben hervorgerufen wurde. Das nächste, und bis dahin deutlichste, Erholungssignal ist etwa ab 2 Millionen Jahren nach dem Aussterben (während des frühen Spathiums) zu beobachten. Während dieses Zeitintervals traten erstmalig eine Mehrzahl höherer Taxa, die typisch für das Mesozoikum sind, gemeinsam auf und bilden damit den Grundstock für die eigentliche Radiation während der Mitteltrias. Der Vergleich beider Untersuchungsgebiete zeigt, dass lokale Stressfaktoren, wie Schwankung in der Salinität, jederzeit das primäre globale Erholungssignal verzerren oder überdecken können. Das abgeleitete Gesamtmuster legt nahe, dass die verzögerte Erholung auf kurze, womöglich aber globale Umweltveränderungen während des oberen Dieneriums zurück zuführen sind.

Der zweite wesentliche Beitrag der vorliegenden Arbeit betrifft die Berücksichtigung intrinsischer Faktoren auf die Erholung. Die Analyse der gut dokumentierten Virgin Formation (Südwest-Utah) haben ergeben, dass viele Arten als Generalisten in verschiedensten Subhabitaten dieser Region vorkamen. Solch ein faunistisches Merkmal wird traditionell als Hinweis für Stressfaktoren interpretiert, was jedoch im Falle der Virgin Formation mit einer relativ hohen Gesamtdiversität und differenzierten Ökosystemstruktur nicht in Einklang zu bringen ist. Alternativ schlagen wir vor, dass der geringe Spezialisierungsgrad benthischer Organismen geringe intraspezifische Konkurrenz widerspiegelt. Nach hinreichend großen Aussterbeereignissen, welche typischerweise eine geringe Habitatdiversität (Alpha-Diversität) hinterlassen, erlaubt die geringe Konkurrenz, dass die relativ wenigen Arten auch außerhalb ihres ökologischen Optimums existieren können. Dies sollte sich in einer kleineren differentiellen Diversität der Habitate untereinander (Beta-Diversität) niederschlagen. Demnach sollte Betadiversität nach einem Massenaussterben erst dann signifikant ansteigen, wenn Alphadiversität ein Niveau erreicht, unter dem das Prinzip des Konkurrenzausschluss als wichtiger Evolutionsmotor zu greifen beginnt. Ein Test dieses Modells für die gesamte hier bearbeitete Untertrias der USA zeigt, dass Betadiversität konstant blieb, während hingegen Alphadiversität kontinuierlich anstieg. Diese könnte eine Erklärung dafür liefern, warum benthische Organismengruppen, wie Bivalven und Gastropoden, erst deutlich nach dem definitiven Einsetzen der Erholung zu radieren begannen. Weiterführende Forschungsarbeiten, die Mitteltriassische und Permische Ökosysteme einbeziehen, sollen die Plausibilität dieses Modells weiter testen. Die generell geringe Biodiversität während der Untertrias wurde immer wieder als Hinweis für umweltbedingte Stressfaktoren angeführt. In der vorliegenden Arbeit heben wir hervor, dass der Zusammenhang zwischen geringer Diversität und ungünstigen Umweltbedingungen im Kontext eines Massenaussterbens möglicherweise seine Anwendbarkeit für paläoökologischen Fragestellungen verliert.

Die vorgelegte Dissertation leistet einen wichtigen Beitrag zur Interpretation von fossilen Ökosystemen der Untertrias und erlaubt damit eine genauere Rekonstruktion der Umweltbedingungen in diesem Zeitintervall. Die beobachteten Daten können erklärt werden durch (i) kurze Phasen von interregional wirkenden Stressfaktoren und (ii) anaktualistische ökologische Effekte, die eine direkte Folge des dramatischen Verlusts an Biodiversität und Zusammenbruch komplexer Ökosystemstrukturen waren.

Schlüsselwörter: Erholung • Benthos • Evolution • Massenaussterben • Untertrias • Bivalven • Paläoökologie

Introduction

The end-Permian mass extinction and Early Triassic recovery

The end-Permian mass extinction represents the most dramatic crises in the History of metazoan life. It has been estimated that up to 96% of marine species went extinct at the end of this period (Raup 1979). Whereas the loss in biodiversity has been recognized quite early (Newell, 1952; Schindewolf, 1954), its causes remained dubious for at least two decades. With respect to various crucial aspects (timing, selectivity, and geochemical signatures), available data were too scant to distil truly testable hypotheses (see Payne and Clapham, 2012). This situation changed dramatically during the eighties of the last century. Global diversity curves based on the Sepkoski (1982) compendium became available to study taxonomic effetcs of extinctions. Geochemical evidence was implemented in palaeontological research to reveal chronologic constraints and underlying processes. In recent decades a number of more or less plausible scenarios have been developed to explain this event. These include regressions (Holser et al., 1989), flood basalt volcanism (Renne et al., 1995; Payne and Kump, 2007), extraterrestrial impacts (Becker et al., 2004), global marine anoxia (Wignall and Twitchett, 1996; Isozaki, 1997), hypercapnia (Knoll et al., 2007), euxinia (Grice et al., 2005; Meyer and Kump, 2008), methane release (Krull and Retallack, 2000), carbon dioxide release via vaporization of coal deposits (Erwin, 2006), and degassing of halocarbons and greenhouse gases caused by the thermal alteration of evaporites and organic-rich sediments (Svensen et al., 2009) during the rise of the Siberian Trap magma. Large quantities of erupted lava would have been directly detrimental to the biosphere. Furthermore, many of the potential kill mechanisms listed above are indirectly or directly linked trap basalt eruptions. Accordingly, there is now some consensus that the Siberian Trap volcanism was the main trigger of the end-Permian mass extinction (Wignall, 2007).

The consequences of this event were first of all a dramatic loss in biodiversity (Fig. 1) and the large scale degradation of ecosystem networks (Erwin, 2001). The extinction moreover altered the taxonomic composition and the ecological structure of the biosphere like no other event since the Cambrian Explosion (Sepkoski, 1981; Bambach et al., 2002). The rise in the dominance of the "Modern evolutionary fauna" on the expense of the "Palaeozoic evolutionary fauna" (Fig. 1, Sepkoski et al., 1981), was probably closely linked to extinction amd ecospace vacation across Permian-Triassic boundary interval. Apart from understanding (selective) kill mechanism during the extinction, the reconstruction of evolutionary pathways of surviving biota in the course of the ensuing recovery interval is of utmost importance for reconstructing the evolution of the modern biosphere.

Another important aspect of the mass extinction and its aftermath is the character of a "natural experiment". Regardless of difficulties in identifying unequivocal cause-and-effect relationships in deep time, historical extinction-recovery couplets provide the only opportunity to address several key questions of evolutionary biology and earth system science: (i) how do ecosystems respond to large-scale environmental stress, (ii) how quickly do ecosystems recover, and (iii) how do evolutionary processes operate under the unusual conditions of vacated ecospace? Stimulated by studies such as Hallam (1991), Wignall and Hallam (1992), or Schubert and Bottjer (1992), the Early Triassic has become a major focus in palaeontological research for now more than two decades.

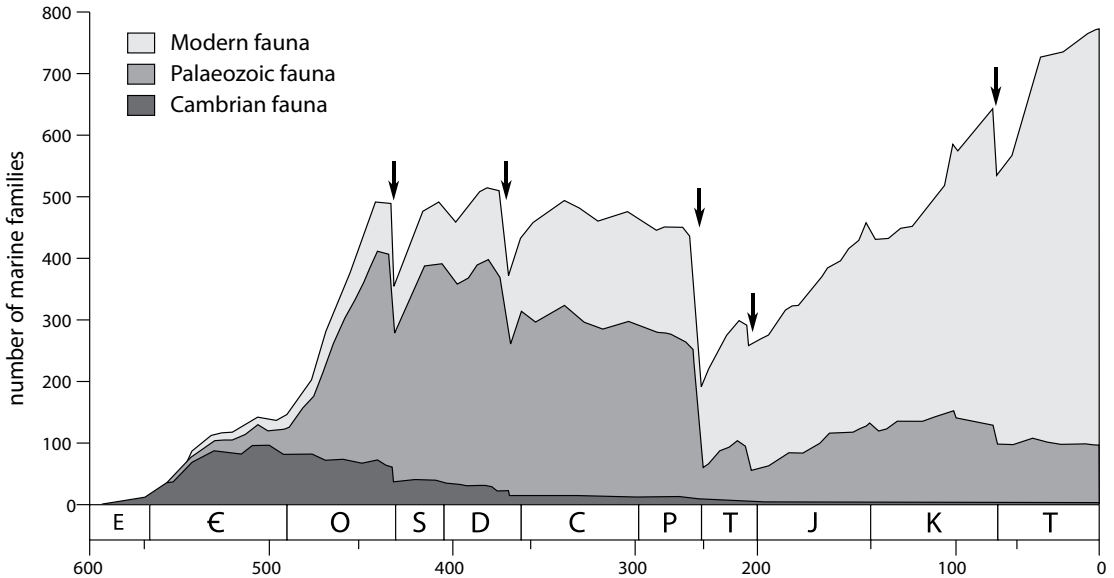

Fig. 1. Marine biodiversity from the Ediacaran to present (after Sepkoski, 1984). E: Ediacaran, Є: Cambrian, O: Ordovician, S: Silurian, D: Devonian, C: Carboniferous, P: Permian, T: Triassic, J: Jurassic, K: Cretaceous, T: Cenozoic (Tertiary). Black arrows indicate that position of the "big five" mass extinction Absolut time scale is not evenly scaled.

Early Triassic benthic ecosystems – A brief historical review

Benthic ecosystems have been in the focus of recovery research (Schubert and Bottjer, 1992; Schubert and Bottjer, 1995; Twitchett and Wignall, 1996) ever since this topic grew in popularity during the mid-1990s. The earliest studies, that particularly employed field-based analysis of benthic ecosystems with respect to recovery as such, were that of Schubert and Bottjer (1995) and Twitchett and Wignall (1996). Twitchett and Wignall (1996) used trace fossils to reconstruct the palaeoecological and environmental conditions throughout the Lower Triassic Werfen Formation of the Dolomites. Their main finding was that ichnodiversity as well as burrowing intensity is highly reduced throughout much of the Formation except for some intervals in the late Griesbachian, and the Spathian. Twitchett and Wignall (1996) related the paucity of bioturbation in the Mazzin Member (Griesbachian) to widespread shallow marine anoxic conditions, and in the Campil Member (Smithian) to salinity fluctuations and thus mainly to extrinsic factors inhibiting infaunal activity. This was one of the first studies (besides Wignall and Hallam, 1992) that presented newly collected field data to support the hypothesis of Hallam (1991) who suggested that the delayed recovery was largely a result of persistent environmental stress (i.e. shallow marine anoxia). Schubert and Bottjer (1995) gave a first overview on the occurrence of benthic palaeo-communities throughout Lower Triassic strata of the western U.S. This study demonstrated that there was apparently no radiation for most of the Early Triassic. In their own words: "cosmopolitan, opportunistic generalists, and low-diversity, low-complexity palaeo-communities were characteristic of the entire Early Triassic in the western USA" (Schubert and Bottjer, 1995, p. 31). Other than Twitchett and Wignall (1996), Schubert and Bottjer (1995) favoured that primary ecological effects account for the patterns observed. Whereas there was essentially consensus on a delay of recovery (Stanley, 1990; Hallam, 1991), the question whether this protraction reflects intrinsic or extrinsic factors is highly debated till today. Attempts have been made to extract general trends of recovery (e.g. Kauffman and Erwin, 1995; Twitchett, 1999). Resulting models were rather descriptive than theoretical and they were used to quantify recovery at new localities (e.g. Twitchett et al., 2004).

During the early two thousands, a considerable number of paper added many aspects to the recovery. Rodland and Bottjer (2001) explored the role of lingulid brachiopods as "disaster taxa" (see also Schubert and Bottjer, 1992). Pruss and Bottjer (2004) analysed trace fossil assemblages from the western U.S. Fraiser et al. (2005) and Twitchett (2007) focused on the small body size which seems typical for Early Triassic marine invertebrates. All of these, and closely related studies (Boyer et al., 2004; Fraiser and Bottjer, 2005; 2007; Kershaw et al., 2007; Mata and Bottjer, 2011), adopted the idea that the failed re-diversification and simplicity in ecosystem structure largely results from ongoing environmental stress. Consequently, faunas that were showing unexpected high diversities (e.g. Krystyn et al., 2003; Beatty, et al., 2008) were interpreted as refugia (Twitchett et al., 2004) in an otherwise hostile environment. However, most papers of this period of research provided no actual palaeoecological data. Similarly unfavourable, most studies were not substantiated by up-to-date systematic descriptions of fossil material nor provided reliable species level identifications. A number of more recent studies exemplified (e.g. Nützel, 2005a, b; Nützel and Schulbert, 2005; Hautmann and Nützel, 2005; McGowan et al., 2009; Kaim et al., 2010; Hautmann et al. 2011) that providing a phylogenetic framework and/or (quantitative) species level data facilitates a much more differentiated discussion. Most of these studies at least partially questioned previous claims on the hostile conditions in the aftermath of the extinction. It becomes apparent that only actual community data of favourably continuous successions will help to elucidate recovery trajectories of benthic ecosystems.

Recent results from geochemical and stratigraphic surveys considerably advanced the understanding of the recovery. Payne et al. (2004) have shown that the Early Triassic witnessed huge fluctuations in the carbon isotope record, which could be explained by two scenarios: (i) repeated environmental perturbations or (ii) fundamental changes in the global carbon cycle as a consequence of ecosystem collapse. The combination of high resolution ammonoid data, absolute U–Pb ages, and carbon cycle perturbations (Ovtcharova et al., 2006; Galfetti et al., 2007, Brayard et al., 2009) revealed some crucial aspects: (i) the first three Early Triassic substages are much shorter than previously suggested (Fig. 2) and (ii) diversity dynamics of ammonoids are linked to carbon isotope fluctuations. This implies that the duration of

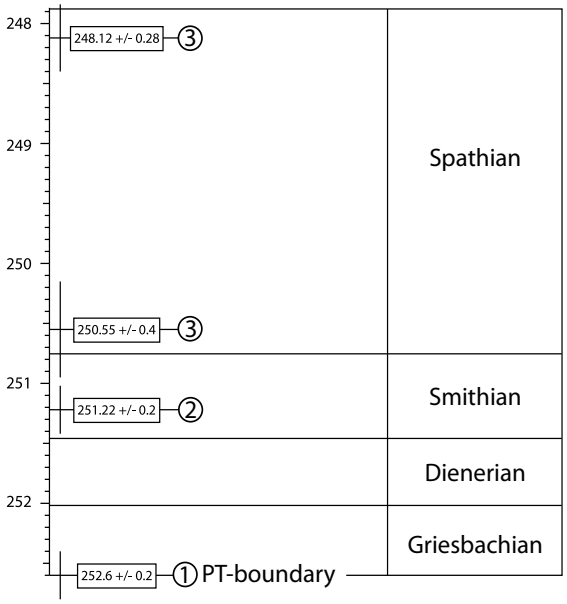

Fig. 2. Early Triassic stage subdivision (Tozer, 1967) calibrated with recently published radiometric ages from South China (1: Mundil et al., 2004; 2: Galfetti et al., 2007; 3: Ovtcharova et al., 2006)

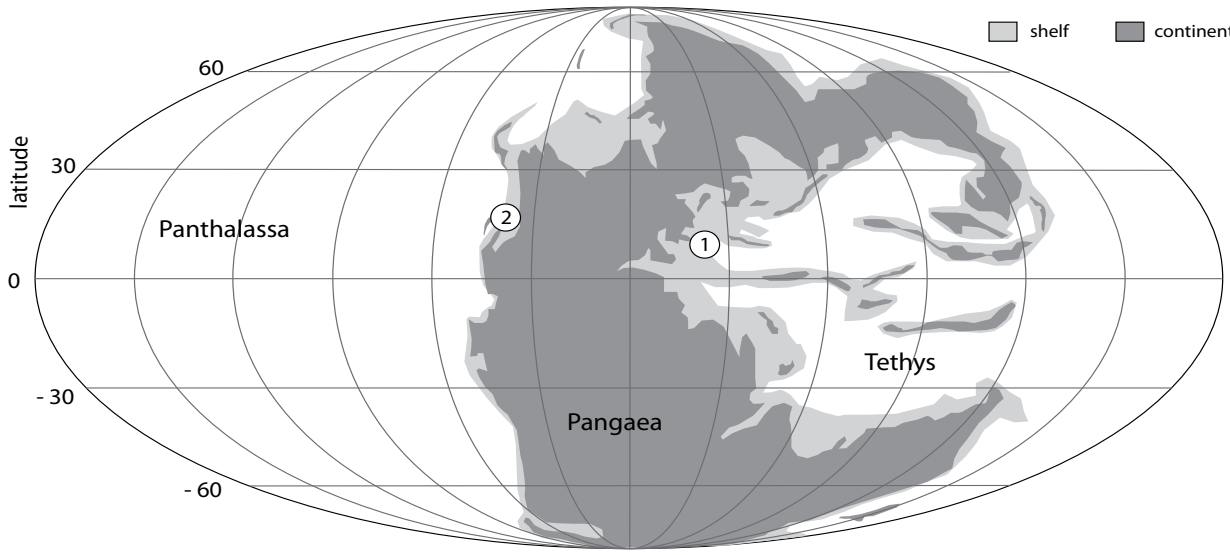

Fig. 3. Early Triassic palaeogeography with study localities (1: southern Alps/Dolomites, 2: western U.S.), after Blakey (2011).

the delay in the recovery was much shorter and that Early Triassic ecosystems were most likely subjected to repeated rather than persistent periods of environmental stress. Orchard (2007) and Brayard et al. (2009) demonstrated that nektonic groups experienced dramatic re-diversifications, which are incompatible with catastrophic scenarios proposed in earlier studies.

Data from benthic ecosystems, which relentlessly fueled the "delay scenario" during the last two decades, now experience a critical re-evaluation. For instance, Hautmann et al. (2011) have shown that diverse benthic ecosystems were not restricted to what has been referred to as refuges (e.g. Krystyn et al., 2003). Stanley (2009) speculated that benthic clades may show a recovery pattern that also follows ups and downs as has been demonstrated for the nekton (see above). The presented thesis attempts to focus the analysis of benthic ecosystems again on actual community data and to embed them within a detailed systematic, stratigraphic and environmental framework whenever possible.

Main objectives and general outline

The main goals of this thesis are to test for early restoration signals and subsequent declines in benthic ecosystems and to revisit the role of intrinsic controls in the recovery which has been largely neglected since Schubert and Bottjer (1995). Field localities include the Lower Triassic units of the Western U.S. and the Werfen Formation of the Dolomites (Italy). Both regions provide a relatively continuous record of tropical shelf settings from the Tethys and the Panthalassa ocean respectively (Fig. 3). By comparing both localities, it is aimed to extract general trends and to distinguish local from global signals. Furthermore, these two localities are of particular interest because they are assumed to record the "worst case scenarios" for Early Triassic recovery (Wignall and Hallam, 1992).

Especially the following questions, which are central to the understanding of the recovery process, were addressed.

• Which benthic communities occurred where and when during the Early Triassic and which taxa and ecological guilds are characteristic?

• Do benthic ecosystems show early recovery signals and subsequent decline and if so, do these trends correspond with changes in environmental parameters and the restoration signals seen in other clades?

• Where there fundamental differences in the recovery between the western Tethys and eastern Panthalassa, and how could they be explained?

• How did parameters such as alpha diversity, beta diversity, guild diversity and dominance of communities change over time? Are any of these changes linked with each other?

• Is it possible to differentiate between extrinsic and intrinsic controls on the recovery?

• Are there any general rules on biodiversity dynamics that can be extracted from the data?

The chapters of the thesis represent published or submitted manuscripts and were conceived as independent contributions. Accordingly, introductions, methods, and some discussion-paragraphs may be repetetive.

In the course of the first two field campaigns carried out in the Southern Alps, a peculiar trace fossil assemblage of the Werfen Formation was discovered and documented. Because the importance of ichnological data has been recognized quite early (Twitchett and Wignall, 1996), it became apparent that these finds provided a first step

toward a revisited understanding of the recovery process. The new material from a known trace fossil locality (Twitchett and Wignall, 1996) is described in **Chapter 1** (Hofmann et al., 2011, published). Based on this as well as on published trace- and body fossil data, the general validity of the hitherto established recovery model (e.g. Twitchett, 1999) and the general chronology of the reappearance of key ichnotaxa is discussed.

The field work in the western U.S. was first successfully accomplished for the well-exposed Virgin Formation (Spathian) of south-western Utah. A most promising aspect of this unit was that it records a variety of shallow to marginal marine sedimentary environments allowing for sampling of benthic organisms from various sub-habitats. In this study, the essential algorithm to reconstruct benthic communities, which was applied in all follow-up studies, was developed. The main objectives of this study (**Chapter 2**, Hofmann et al., 2013a, published) were (i) to reconstruct the benthic associations of the Virgin Formation based on species level identification (following Hautmann et al., 2013), (ii) to extract unequivocal recovery signals from "noise-variation" merely reflecting the environmental heterogeneity of shallow-marine environments, and finally (iii) to quantify the degree of faunal heterogeneity between sub-environments and thus assessing the role of beta diversity in the post-extinction diversity increase.

Although Schubert and Bottjer (1995) included some quantitative genus-level collections of the Dinwoody Formation (Griesbachian-Dienerian, western U.S.) in their seminal paper, the palaeoecological situation as well as recovery patterns recorded by this unit have never been satisfactorily explored. **Chapter 3** (Hofmann et al., 2013b, published) provides a systematic description of the benthic macrofauna (including bivalves, gastropods, and brachiopods), and comprehensive palaeoecological analysis. The spatial and temporal distribution of benthic associations allows for testing the diversity-partitioning recovery model proposed in chapter 2. In connection to this, the importance of intrinsic controls on the notoriously low-diverse associations of the early post-extinction faunas is discussed.

Chapter 4 (Hofmann et al., 2013c, published online) focuses on the Thaynes Group and the roughly coeval Sinbad Formation of the western U.S. These units were already studied in terms of palaeoecology by Schubert and Bottjer (1995) but only with a low stratigraphic and systematic resolution. This paper presents a comprehensive systematic description (including bivalves, brachiopods, and gastropods) and an accompanying palaeoecological analysis as performed in Chapter 3 and 4. The correlation with a new high-resolution ammonoid zonation allowed for a reconstruction of recovery trajectories throughout the Smithian time interval and across the important Smithian-Spathian boundary. In the last part, a comprehensive review of all studied Lower Triassic units of the western U.S. was carried out providing a summary on the benthic recovery at the tropical eastern Panthalassa margin. This paper also explores when and to which extent benthic ecosystems were affected by environmental stress of interregional impact. Finally, a conclusive test on the validity of the diversity-partitioting recovery model as proposed in chapter 2 is presented for the Early Triassic.

The Werfen Formation of the Dolomites (Italy) has a rich historic record of palaeontological research and was also early recognised as a key locality for post-extinction studies (Twitchett and Wignall, 1996). Quite surprisingly, a comprehensive analysis of its abundant benthic macro fauna has not been attempted yet. **Chapter 5** (scheduled to be submitted to *Lethaia*) closes this gap by providing a palaeoecological analysis as performed in chapters 2–4. The stratigraphic distribution of benthic association was used to track the evolution and diversity dynamics of the recovery in the western tropical Thethys. Finally, this chapter compares both, the western Tethys and the eastern Panthalassa, signals.

References

Bambach, R. K., A. H. Knoll, AND J. J. Sepkoski. 2002. Anatomical and ecological constraints on Phanerozoic animal diversity in the marine realm. Proceedings of the National Academy of Sciences of the United States of America, 99(10):6854-6859.

Beatty, T.W., Zonneveld, J.P. and Henderson, C.M., 2008. Anomalously diverse Early Triassic ichnofossil assemblages in Northwest Pangea: A case for a shallow-marine habitable zone. Geology, 36(10): 771-774.

Becker, L., Poreda, R.J., Basu, A.R., Pope, K.O., Harrison, T.M., Nicholson, C., Iasky, R., 2004. Bedout: A possible end-Permian impact crater offshore of Northwestern Australia. Science 304, 1469-1476.

Blakey, R.C. 2011. Colorado Plateau Stratigraphy and Geology and Global and Regional Paleogeography. http://www2.nau.edu/rcb7/index.html. (February 2011).

Boyer, D.L., Bottjer, D.J., and Droser, M.L. 2004. Ecological Signature of Lower Triassic Shell Beds of the Western United States. Palaios 19 (4): 372-380.

Brayard, A. et al., 2009. Good Genes and Good Luck: Ammonoid Diversity and the End-Permian Mass Extinction. Science, 325(5944): 1118-1121.

Erwin, D.H. 2001. Lessons from the past: Biotic recoveries from mass extinctions. Proceedings of National Academy of Science 98: 5399-5403.

Erwin, D. H. 2006. Extinction: How Life on Earth Nearly Ended 250 Millions Years Ago. Princeton University Press, 296 p.

Fraiser, M.L. and Bottjer, D.J., 2005. Restructuring in benthic level-bottom shallow marine communities due to prolonged environmental stress following the end-Permian mass extinction. Comptes Rendus Palevol, 4(6-7): 583-591.

Fraiser, M.L. and Bottjer, D.J., 2007. Elevated atmospheric CO2 and the delayed biotic recovery from the end-Permian mass extinction. Palaeogeography Palaeoclimatology Palaeoecology, 252(1-2): 164-175.

Fraiser, M.L., Twitchett, R.J., Bottjer, D.J., 2005. Unique microgastropod biofacies in the Early Triassic: Indicator of long-term biotic stress and

the pattern of biotic recovery after the end-Permian mass extinction. Cr Palevol 4, 543-552.

Galfetti, T. et al., 2007. Timing of the Early Triassic carbon cycle perturbations inferred from new U-Pb ages and ammonoid biochronozones. Earth and Planetary Science Letters, 258(3-4): 593-604.

Grice, K., Cao, C.Q., Love, G.D., Bottcher, M.E., Twitchett, R.J., Grosjean, E., Summons, R.E., Turgeon, S.C., Dunning, W., Jin, Y.G., 2005. Photic zone euxinia during the Permian-Triassic superanoxic event. Science 307, 706-709.

Hallam, A., 1991. Why was there a delayed radiation after the end-Palaeozoic extinctions? Historical Biology, 5: 257 – 262.

Hautmann, M., Bucher, H., Brühwiler, T., Goudemand, N., Kaim, A., and Nützel, A. 2011. An unusually diverse mollusk fauna from the earliest Triassic of South China and its implications for benthic recovery after the end-Permian biotic crisis. Geobios 44(1): 71-85.

Hautmann, M., Smith, A. B., McGowan, A. J. and Bucher, H. 2013. Bivalves from the Olenekian (Early Triassic) of southwestern Utah: Systematics and evolutionary significance. - Journal of Systematic Palaeontology 11(3): 263-293.

Hautmann, M. and Nützel, A. 2005. First record of a heterodont bivalve (Mollusca) from the Early Triassic: Palaeoecological significance and implications for the 'Lazarus problem'. Palaeontology 48(2): 1131-1138.

Hofmann, R., Goudemand, N., Wasmer, M., Bucher, H. and Hautmann, M. 2011. New trace fossil evidence for an early recovery signal in the aftermath of the end-Permian mass extinction. Palaeogeography, Palaeoclimatology, Palaeoecology. 310 (3-4): 216-226.

Hofmann, R., Hautmann, M., Wasmer, M., Bucher, H., 2013a. Palaeoecology of the Spathian Virgin Formation (Utah, USA) and Its Implications for the Early Triassic Recovery. Acta Palaeontologica Polonica 58, 149-173.

Hofmann, R., Hautmann, M., Bucher, H. 2013b: A new paleoecological look at the Dinwoody Formation (Lower Triassic, western U.S.): intrinsic versus extrinsic controls on ecosystem recovery after the end-Permian mass extinction. Journal of Paleontology. 87(5): 854-880.

Hofmann, R., Hautmann, M., Brayard, A., Nützel, A., Bylund, K. G., Jenks, J. F., Vennin, E., Olivier, N., Bucher, H., 2013c: Recovery of benthic marine communities from the end-Permian mass extinction at the low latitudes of eastern Panthalassa. Palaeontology. Early View, 11 Oct 2013, doi: 10.1111/pala.12076.

Holser, W.T., Schonlaub, H.P., Attrep, M., Boeckelmann, K., Klein, P., Magaritz, M., Orth, C.J., Fenninger, A., Jenny, C., Kralik, M., Mauritsch, H., Pak, E., Schramm, J.M., Stattegger, K., Schmoller, R., 1989. A Unique Geochemical Record at the Permian Triassic Boundary. Nature 337, 39-44.

Isozaki, Y., 1997. Timing of Permian-Triassic anoxia. Science 277, 1748-1749.

Kaim, A., Nutzel, A., Bucher, H., Bruhwiler, T. and Goudemand, N., 2010. Early Triassic (Late Griesbachian) gastropods from South China (Shanggan, Guangxi). Swiss Journal of Geosciences, 103(1): 121-128.

Kauffman, E.G., and Erwin, D.H., 1995. Surviving mass extinctions. Geotimes 14, 14-17.

Kershaw, S., Li, Y., Crasquin-Soleau, S., Feng, Q.L., Mu, X.N., Collin, P.Y., Reynolds, A., Guo, L., 2007. Earliest Triassic microbialites in the South China block and other areas: controls on their growth and distribution. Facies 53, 409-425.

Knoll, A.H., Barnbach, R.K., Payne, J.L., Pruss, S., Fischer, W.W., 2007. Paleophysiology and end-Permian mass extinction. Earth and Planetary Science Letters 256, 295-313.

Krull, E.S., Retallack, G.J., 2000. delta C-13 depth profiles from paleosols across the Permian-Triassic boundary: Evidence for methane release. Geological Society of America Bulletin112, 1459-1472.

Krystyn, L., Richoz, S., Baud, A. and Twitchett, R.J., 2003. A unique Permian-Triassic boundary section from the Neotethyan Hawasina Basin, Central Oman Mountains. Palaeogeography Palaeoclimatology Palaeoecology, 191(3-4): 329-344.

Mata, S.A. and Bottjer, D.J. 2011. Origin of Lower Triassic microbialites in mixed carbonate-siliciclastic successions: Ichnology, applied stratigraphy, and the end-Permian mass extinction. Palaeogeography, Palaeoclimatology, Palaeoecology 300 (1-4): 158-178.

Mcgowan, A.J., Smith, A.B. and Taylor, P.D., 2009. Faunal diversity, heterogeneity and body size in the Early Triassic: testing post-extinction paradigms in the Virgin Limestone of Utah, USA*. Australian Journal of Earth Sciences, 56(6): 859-872.

Meyer, K.M., Kump, L.R., 2008. Oceanic euxinia in Earth history: Causes and consequences. Annual Review of Earth and Planetary Sciences 36, 251-288.

Mundil, R., Ludwig, K.R., Metcalfe, I., and Renne, P.R. 2004. Age and Timing of the Permian Mass Extinctions: U/Pb Dating of Closed-System Zircons. Science 305: 1760-1763.

Newell, N. D. 1952. Periodicity in Invertebrate Evolution. Journal of Paleontology, 26(3):371-385.

Nützel, A., Schulbert, C., 2005. Facies of two important Early Triassic gastropod lagerstatten: implications for diversity patterns in the aftermath of the end-Permian mass extinction. Facies 51, 480-500.

Nützel, A. 2005. Recovery of gastropods in the Early Triassic. Comptes Rendus Palevol, 4(6-7):501-515.

Nützel, A., 2005. A new Early Triassic gastropod genus and the recovery of gastropods from the Permian/Triassic extinction. Acta Palaeontologica Polonica 50, 19-24.

Orchard, M.J., 2007. Conodont diversity and evolution through the latest Permian and Early Triassic upheavals. Palaeogeography Palaeoclimatology Palaeoecology, 252(1-2): 93-117.

Ovtcharova, M. et al., 2006. New Early to Middle Triassic U-Pb ages from South China: Calibration with ammonoid biochronozones and implications for the timing of the Triassic biotic recovery. Earth and Planetary Science Letters, 243(3-4): 463-475.

Payne, J.L., Clapham, M.E., 2012. End-Permian Mass Extinction in the Oceans: An Ancient Analog for the Twenty-First Century? Annual Review of Earth and Planetary Sciences 40, 89-111.

Payne, J.L., Kump, L.R., 2007. Evidence for recurrent Early Triassic massive volcanism from quantitative interpretation of carbon isotope fluctuations. Earth and Planetary Science Letters 256, 264-277.

Payne, J.L., Lehrmann, D.J., Wei, J.Y., Orchard, M.J., Schrag, D.P., Knoll, A.H., 2004. Large perturbations of the carbon cycle during recovery from the end-Permian extinction. Science 305, 506-509.

Pruss, S.B. and Bottjer, D.J., 2004. Early triassic trace fossils of the western United States and their implications for prolonged environmental stress from the end-Permian mass extinction. Palaios, 19(6): 551-564.

Raup, D.M., 1979. Size of the Permo-Triassic Bottleneck and Its Evolutionary Implications. Science 206, 217-218.

Renne, P.R., Zhang, Z.C., Richards, M.A., Black, M.T., Basu, A.R., 1995. Synchrony and Causal Relations between Permian-Triassic Boundary Crises and Siberian Flood Volcanism. Science 269, 1413-1416.

Rodland, D.L., Bottjer, D.J., 2001. Biotic recovery from the end-permian mass extinction: Behavior of the inarticulate brachiopod Lingula as a disaster taxon. Palaios 16, 95-101.

Schindewolf OH. 1954. Über die mÖglichen Ursachen der grossen erdgeschichtlichen Faunenschnitte. Neues Jahrb. Geol. Palaeontol. Monatshefte 10:457–65.

Schubert, J.K., Bottjer, D.J., 1992. Early Triassic Stromatolites as Post Mass Extinction Disaster Forms. Geology 20, 883-886.

Schubert, J.K. and Bottjer, D.J., 1995. Aftermath of the Permian-Triassic Mass Extinction Event - Paleoecology of Lower Triassic Carbonates in the Western USA. Palaeogeography Palaeoclimatology Palaeoecology, 116(1-2): 1-39.

Sepkoski, J.J. Jr. 1982. A compendium of fossil marine families. Milwaukee Public Museum Contributions in Biology and Geology 51:1-125.

Sepkoski, J.J.Jr., Bambach, R.K., Raup, D.M., Valentine, J.W., 1981. Phanerozoic Marine Diversity and the Fossil Record. Nature 293, 435-437.

Sepkoski, J.J.Jr, 1984. A Kinetic-Model of Phanerozoic Taxonomic Diversity .3. Post-Paleozoic Families and Mass Extinctions. Paleobiology 10, 246-267.

Stanley, S.M., 1990. Delayed Recovery and the Spacing of Major Extinctions. Paleobiology 16, 401-414.

Stanley, S.M., 2009. Evidence from ammonoids and conodonts for multiple Early Triassic mass extinctions. Proceedings of the National Academy of Sciences of the United States of America, 106(36): 15264-15267.

Svensen, H. et al., 2009. Siberian gas venting and the end-Permian environmental crisis. Earth and Planetary Science Letters, 277(3-4): 490-500.

Twitchett, R.J., 1999. Palaeoenvironments and faunal recovery after the end-Permian mass extinction. Palaeogeography Palaeoclimatology Palaeoecology, 154(1-2): 27-37.

Twitchett, R.J., 2007. The Lilliput effect in the aftermath of the end-Permian extinction event. Palaeogeography Palaeoclimatology Palaeoecology 252, 132-144.

Twitchett, R.J. and Wignall, P.B., 1996. Trace fossils and the aftermath of the Permo-Triassic mass extinction: Evidence from northern Italy. Palaeogeography Palaeoclimatology Palaeoecology, 124(1-2): 137-151.

Twitchett, R.J., Krystyn, L., Baud, A., Wheeley, J.R. and Richoz, S., 2004. Rapid marine recovery after the end-Permian mass-extinction event in the absence of marine anoxia. Geology, 32(9): 805-808.

Wignall, P.B. and Hallam, A., 1992. Anoxia as a Cause of the Permian Triassic Mass Extinction - Facies Evidence from Northern Italy and the Western United-States. Palaeogeography Palaeoclimatology Palaeoecology, 93(1-2): 21-46.

Wignall, P.B. and Twitchett, R.J., 1996. Oceanic anoxia and the end Permian mass extinction. Science, 272(5265): 1155-1158.

Wignall, P.B., 2007. The End-Permian mass extinction - how bad did it get? Geobiology 5, 303-309.

Chapter 1

New trace fossil evidence for an early recovery signal in the aftermath of the end-Permian mass extinction

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"Most of my sweet memories
were buried in the sand.
The fire and the pain
will now be coming to an end.

How did you get to save me
from this desolate wasteland.
In your eyes I see the dawn
of brighter days again."

from "Wasteland" by Woodkid
Album: Golden Age
Green United Music (2013)

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New trace fossil evidence for an early recovery signal in the aftermath of the end-Permian mass extinction

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ABSTRACT

New ichnological data from the Lower Triassic Werfen Formation (Dolomites, Italy) revealed an unexpectedly diverse and complex ichnofauna in mixed siliclastic–carbonate shelf sediments of the western tropical Tethys shortly after the end-Permian mass extinction event. Common elements are *Thalassinoides*, *Palaeophycus* and *Planolites*. Other associated ichnogenera include *Spongeliomorpha*, *Rhizocorallium*, *Lockeia*, *Catenichnus*, *Helminthopsis*, and *Taenidium*. One structure is tentatively determined as *Curvolithus*. Biostratigraphic data (conodonts and bivalves) of the trace fossil interval (lower Seis/Siusi Member) suggest a late Griesbachian age, less than 1 Ma after the end-Permian mass extinction event. Similarly diverse ichnofossil communities from this time interval have recently been described from the Boreal Realm, but this is the first record of a diverse Griesbachian ichnoassemblage from the tropics, indicating that the early recovery of trace fossil producers was not latitudinally restricted, as previously proposed. Accordingly, relatively advanced recovery stages were reached on a global scale much earlier than the Spathian as is commonly acknowledged. The early and interregional peak in ichnofaunal recovery implies subsequent ecological setbacks in post-Griesbachian times that explain the overall delay of benthic recovery until the Spathian. Rather than persistent catastrophic conditions during the Griesbachian, a global and synchronous succession of crises and relaxation phases after the Griesbachian is proposed as an explanatory model for the recovery pattern of benthic ecosystems.

1. Introduction

In recent years, the aftermath of the end-Permian mass extinction has attracted particular attention, because it provides insight into evolutionary dynamics under the unusual conditions of a largely vacated ecospace and helps to better understand biotic response to massive environmental perturbations (Brayard et al., 2009). Besides the analysis of body fossil faunas, trace fossils were considered as an important tool to track environmental changes and the restoration of benthic ecosystems during the recovery interval (Twitchett and Wignall, 1996; Pruss and Bottjer, 2004; Twitchett and Barras, 2004; Beatty et al., 2008; Fraiser and Bottjer, 2009). Ichnological data such as tiering, ichnotaxonomic composition, burrow depth and burrow diameter are widely used to reconstruct ecological conditions and, in particular, bottom water oxygenation in marine sedimentary rocks (Bromley and Ekdale, 1984; Savrda and Bottjer, 1986). For example, tiered ichnocoenoses, large burrow dimensions, and the presence of some trace fossils such as *Thalassinoides*, are considered as reliable indicators of stable ecological and well-oxygenated conditions in marine facies (Bromley and Ekdale, 1984). This relationship has been utilized to characterize recovery stages in the aftermath of the end-Permian mass extinction event (Twitchett, 2006) and the global distribution of certain ichnotaxa is crucial in understanding the spatial and temporal nature of the recovery process (Twitchett and Barras, 2004).

The uppermost Permian to Lower Triassic Werfen Formation of the Dolomites (South Tyrol/ Italy) represents a classic record of the aftermath of the end-Permian mass extinction. A first analysis of the post-extinction ichnofauna (Twitchett and Wignall, 1996) has shown that the lower part of the Werfen Formation yields a generally sparse trace fossil record apart from a short peak in trace fossil diversity and bioturbation in upper Griesbachian strata. However, it has been noted by Twitchett and Wignall (1996) that this trace fossil peak-interval lacks robust trace fossil assemblages including *Thalassinoides*, *Rhizocorallium*, and *Ophiomorpha* that are otherwise typically found in shallow-marine shelf environments (Enos, 1983). The presumed absence of these distinctive ichnotaxa led to the hypothesis of a rather slow and gradual increase in ichnodiversity, burrow size, depth of bioturbation, and ichnofabric index in the aftermath of the end-Permian mass extinction (Twitchett, 1999). It has been also assumed that the reappearance of certain ichnotaxa is of chronologic significance, at least among comparable palaeo-latitudes (Twitchett and Barras, 2004). From the upper Griesbachian part of the Werfen Formation, we report new occurrences of *Thalassinoides*, *Spongeliomorpha*, and *Rhizocorallium* that notably predate the first known occurrences of such key ichnotaxa (Twitchett, 2006) within the palaeotropics. Comparable ichnoassemblages were previously considered to be absent in low-latitudes until

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the late Early Triassic (Spathian) (Pruss and Bottjer, 2004; Twitchett and Barras, 2004), at least 2 million years after the extinction (Ovtcharova et al., 2006; Galfetti et al., 2007).

2. Geological setting and stratigraphic context of the lower Werfen Formation

Fieldwork conducted in summer 2009 focused on a, previously undescribed section at the Aferer Geisler and on a section at the Rosengarten/Catinaccio (Fig. 1a). Both localities provide a continuous and particularly fossiliferous record of the lower Werfen Formation, which was deposited predominantly under shallow marine conditions (Broglio Loriga et al., 1983) at the western margin of the tropical Tethys (Fig. 1b). In these sections, the Werfen Formation (Fig. 2a) reaches a thickness of 110 m and includes the following lithostratigraphic units: Tesero Member, Mazzin Member, Andraz Member, Seis/Siusi Member, Gastropod Oolite Member, and the lower part of the Campil Member. The general depositional setting of the lower Werfen Formation is interpreted as a storm-dominated carbonate shelf environment with occasional siliciclastic input. Predominating lithotypes of the lower Werfen Formation are laminated marly mudstone and occasionally thin beds of wackestone and grainstone, which were deposited in inner shelf and proximal outer shelf settings (Broglio Loriga et al., 1983). Regressive phases are recorded by dolostones and siltstones of intertidal and supratidal environments (Broglio Loriga et al., 1983; Twitchett and Wignall, 1996). The new trace fossils are found in an approximately six meter thick interval composed of light gray to yellowish, laminated to thinly-bedded and partly marly mudstones in the lower part of the Seis/Siusi Member (Fig. 2a). Intercalations of thin-bedded, fine-grained, highly calcareous sandstones are observed locally (Fig. 2d). This lithofacies is interpreted as a lower shoreface to offshore transition environment. The co-occurrence of the bivalve *Claraia clarai* (Fig. 2c) with the observed ichnofauna indicates a late Griesbachian to early Dienerian age (Posenato, 2008). Conodont samples collected about 1 m below and within the first meter of this interval yielded ramiform elements of *Hadrodontina aequabilis* and small elements of *Isarcicella staeschei* (Fig. 2b). This is in agreement with previous studies (see review in Posenato, 2008) suggesting that this interval is of (late) Griesbachian age.

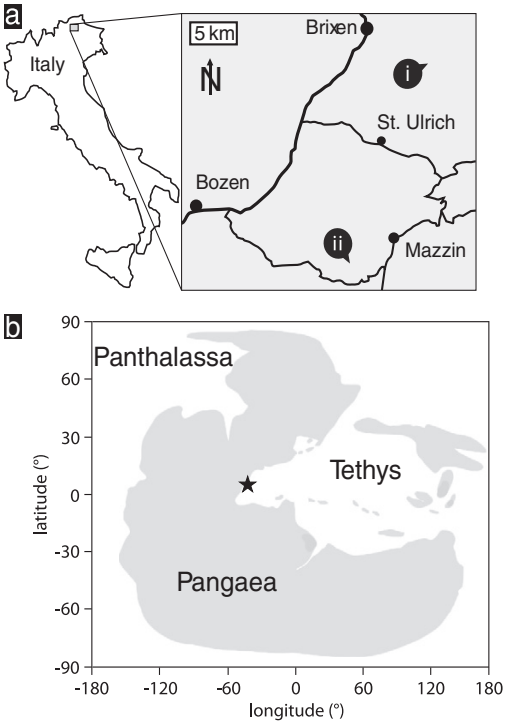

Fig. 1. a: Study area with the investigated localities; i: Aferer Geisler, ii: Catinaccio/Rosengarten. b: Palaeogeographic map of the Early Triassic after Péron et al. (2005). Black star indicates the position of the Dolomite region.

3. New ichnological data from the Werfen Formation

3.1. General characterization of the Seis/Siusi ichnofauna

The ichnofauna from the lower part of the Seis/Siusi Member is dominated by horizontal dwelling and feeding burrows and represents the *Cruziana* ichnofacies *sensu* Seilacher (1967) and McIlroy (2004). The most common trace fossils are infaunal dwelling burrows (*Palaeophycus tubularis*, Fig. 3a), dwelling and feeding burrows of crustaceans such as *Thalassinoides* cf. *suevicus* (Fig. 3b–d), and infaunal deposit-feeding structures (*Planolites montanus*, Fig. 3a). Also present but not particularly abundant are dwelling burrows such as *Spongeliomorpha* isp. (Fig. 4a), *Rhizocorallium* isp. (Fig. 4b), the bivalve resting traces *Lockeia* isp. (Fig. 4c), and *Catenichnus contentus* (Fig. 4d). Observed deposit-feeding structures include *Taenidium barretti* (Fig. 4e) and *Helminthopsis* cf. *abeli* (Fig. 4f). One questionable structure is tentatively identified as *Curvolithus* (Fig. 4g). Comparatively well preserved specimens of horizontal burrows are provided by abundant float material. Furthermore, large slabs from float were chosen to ascertain the bedding plane bioturbation index bpbi (Miller and Smail, 1997), which ranges from bpbi 2 to bpbi 4. Cross sectional outcrop views (Fig. 2d) were suitable to identify vertical structures and to assess ichnofabric indices (Droser and Bottjer, 1986), which range from ii1 to ii4, but is most commonly ii3. All trace fossils described herein were recorded in the same lithology, and different traces co-occur on single slabs. With a recorded number of ten ichnogenera, this ichnoassemblage is notably diverse for the Early Triassic *sensu* Beatty et al. (2008) and furthermore shares characteristic ichnogenera (*Thalassinoides*, *Rhizocorallium* and *Spongeliomorpha*) with ichnofaunas reported from the Boreal Realm by Beatty et al. (2008). The trace fossil diversity of the lower Werfen Formation is not fundamentally different from that reported by Zonneveld et al. (2010) for the Boreal of North America.

3.2. Brief description of the ichnofauna

3.2.1. *Catenichnus contentus* McCarthy, 1979

Material. Five specimens observed in the field (Fig. 4d), Rosengarten section.

Description. Vertical, cylindrical, more or less U-shaped burrow with poorly developed retrusive spreiten. Arms are not parallel and highly diverging. Burrow diameter is 5 mm and width ranges from 35 to 48 mm. Depth of the burrow is 12 mm (terminology after Fürsich, 1974a).

Remarks. Catenichnus differs from the similar ichnogenera *Diplocraterion* and *Arenicolites* in lacking parallel arms. However, similar highly diverging U-shaped burrows lacking spreiten were included in *Arenicolites* (e.g. Mángano et al., 2002). McCarthy (1979) accommodated burrows, both with and without spreiten-structures in this ichnogenus. Accordingly, to synonymize these forms is problematic and we suggest to retain *Catenichnus* as a stable ichnogenus. Furthermore, *Catenichnus* tends to be considerably deeper than wide (ratio 1:4) and is suggested to have been formed during a single excavation episode (McCarthy, 1979; Fillion and Pickerill, 1990). *Catenichnus contentus* is the only ichnospecies of *Catenichnus* and our material corresponds readily with the diagnosis provided by McCarthy (1979).

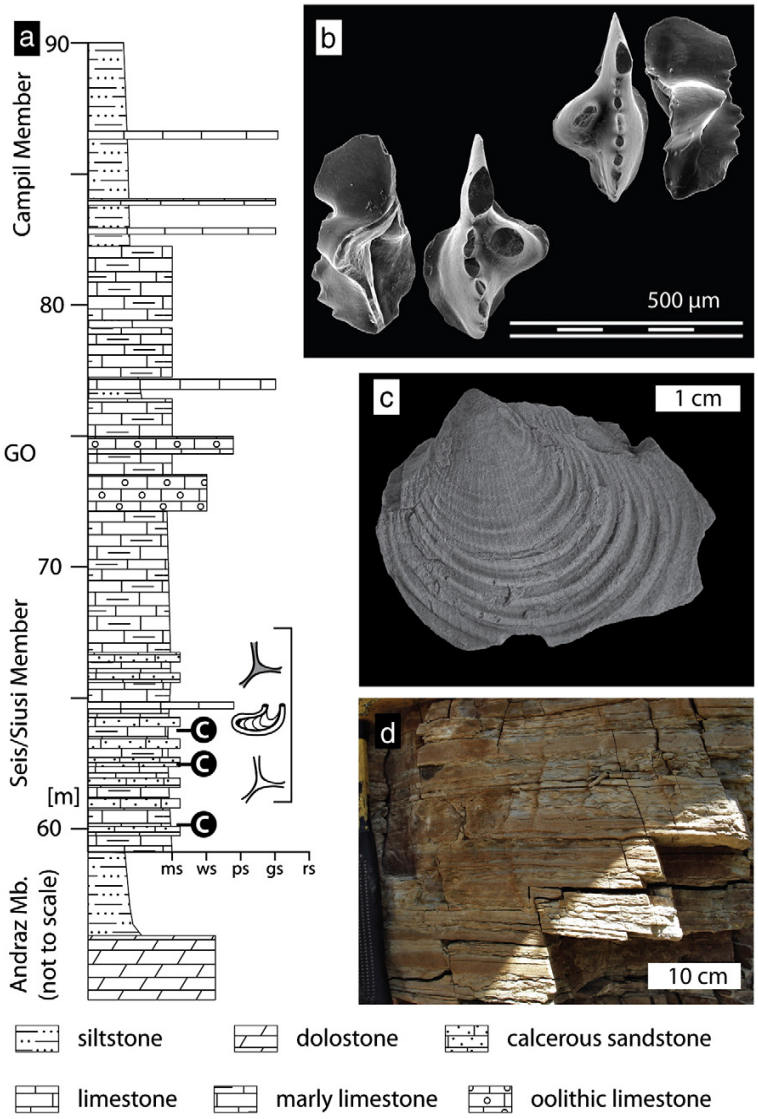

Fig. 2. a: Stratigraphic section of the investigated interval from the Rosengarten locality. Mb.: Member GO: Gastropod Oolite, ms: mudstone, ws: wackestone, ps: packstone, gs: grainstone, rs: rudstone. C: beds sampled for conodonts. b: *Isarcicella staeschei* extracted from rock samples of the trace fossil interval. c: Specimen of *Claraia clarai* from this interval. d: Outcrop photography from the lower Seis/Siusi Member showing intercalated calcarenite and fine-grained sandstone (Rosengarten/Catinaccio section).

Catenichnus is interpreted as a dwelling burrow of suspension-feeders (McCarthy, 1979). This ichnogenus ranges in age from the late Cambrian (Fillion and Pickerill, 1990) to the Early Triassic (Twitchett and Wignall, 1996) and seems to be limited to moderate and high energy shallow-marine environments (McCarthy, 1979; Fillion and Pickerill, 1990). Twitchett and Wignall (1996) reported the ichnogenus from the same stratigraphic level of the Werfen Formation.

3.2.2. *Curvolithus? isp.*

Material. One specimen observed in the field (Fig. 4g), Rosengarten section.

Description. The specimen found in the lower Seis/Siusi Member is preserved as full relief structure at the base of a limestone bed. The burrow is 30 mm wide, 80 mm long and slightly curved.

Remarks. Curvolithus comprises ribbon like, flattened, interstratal traces, which show a characteristic multilobate morphology (Buatois et al., 1998a). The specimen is poorly preserved, which leads to a tentative identification only. Alternatively, this specimen can be interpreted as *Spongeliomorpha*, although branching is not observed and possible ornamentation is poorly developed.

Curvolithus is produced by infaunal carnivores, possibly gastropods, flatworms, or nemerteans (Buatois et al., 1998a). Although this ichnogenus is reported from various marine environments it seems to be a characteristic element of subtidal settings and of the *Cruziana* ichnofacies (Buatois et al., 1998a). It ranges in age from the late Precambrian (Webby, 1970) to the Miocene (Keij, 1965).

3.2.3. *Helminthopsis cf. abeli Książkiewicz, 1977*

Material. One specimen observed in the field (Fig. 4f), Rosengarten section.

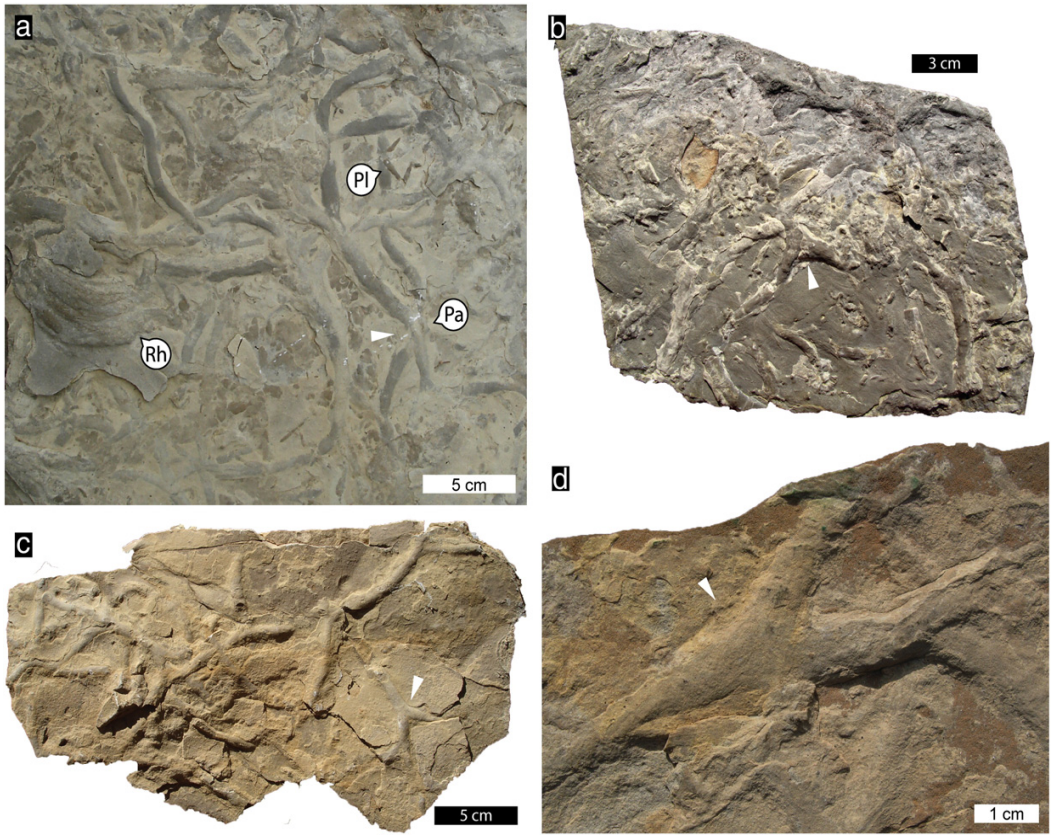

Fig. 3. Trace fossils from the lower Seis/Siusi Member a: Lower bedding plane surface showing intense bioturbation (bpbi = 4) dominated by *Palaeophycus* (Pa), and *Planolites* (Pl). Note the oblique array of spreiten-structures most likely attributable to *Rhizocorallium* (Rh). Branching in *Palaeophycus* represent false branching (white arrow) due to specimen overlap (Rosengarten/Catinaccio). b: *Thalassinoides* cf. *suevicus* showing swelling (white arrow) at the sites of branching (Aferer Geisler). c: Slab with *Thalassinoides* cf. *suevicus* showing characteristic bifurcuations (white arrow), (Rosengarten/Catinaccio). d: *Thalassinoides* cf. *suevicus* showing characteristic bifurcation and swelling (white arrow) at the point of branching (Rosengarten/Catinaccio).

Description. Horizontal sub-cylindrical burrow, following a slightly irregularly meandering course. Burrow diameter is 4 mm.

Remarks. We follow the ichnotaxonomic revision of the ichnogenus *Helminthopsis* provided by Wetzel and Bromley (1996). Our material is best accommodated in *H. abeli*, which is characterized by irregular, open meanders and horseshoe-like turns (Wetzel and Bromley, 1996). However, the last feature is not observed in the specimen, and due to its incomplete preservation we keep it in open nomenclature.

Helminthopsis is interpreted as a deposit-feeding structure (Buatois et al., 1998b) and regarded to have been produced by polychaetes and probably priapulids (Fillion and Pickerill, 1990), at least for marine occurrences (but see Buatois et al., 1998b). It ranges in age from late Precambrian (Gibson, 1989) to the Holocene (Swinbanks and Murray, 1981). *Helminthopsis* is usually recorded in deep-marine settings (Książkiewicz, 1977) but is essentially an eurybathic ichnotaxon occurring in various environments such as shallow-marine (Fillion and Pickerill, 1990), brackish, and non-marine subaqueous environments (Buatois et al., 1998b).

3.2.4. *Lockeia* isp.

Material. Ten specimens observed in the field (Fig. 4c), Rosengarten section.

Description. Almond-shaped traces that are typically preserved as convex hyporelief. Length ranges from 12 to 15 mm and width from 6 to 8 mm. The depth of the figured specimen is 2 mm. Surface is smooth.

Remarks. The most widely reported ichnospecies of *Lockeia* is *Lockeia siliquaria*, which comprises smooth, almond-shaped structures which typically show a tapered and a more rounded end (Mángano et al., 2002). Although the specimens observed in the field would be best accommodated in *L. siliquaria*, they are too indistinct to allow unequivocal ichnospecies identification.

Lockeia is a resting trace typically produced by bivalves (Seilacher, 1953). The ichnogenus ranges in age from the late Cambrian/early Ordovician (Fillion and Pickerill, 1990) to the Pleistocene (Pemberton and Jones, 1988). *Lockeia* is a facies-crossing form and present in all marine and freshwater environments (Mángano et al., 2002 and references therein). The ichnogenus has already been reported from the Seis/Siusi Member (Twitchett and Wignall, 1996).

3.2.5. *Palaeophycus tubularis* Hall, 1847

Material. Approximately 50 specimens observed in the field (Fig. 3a), Rosengarten section.

Description. Straight to irregularly sinusoidal, horizontal, thinly lined cylindrical burrows, preserved as both positive and negative epi- and hyporeliefs. Surface is generally smooth. Fill is massive and

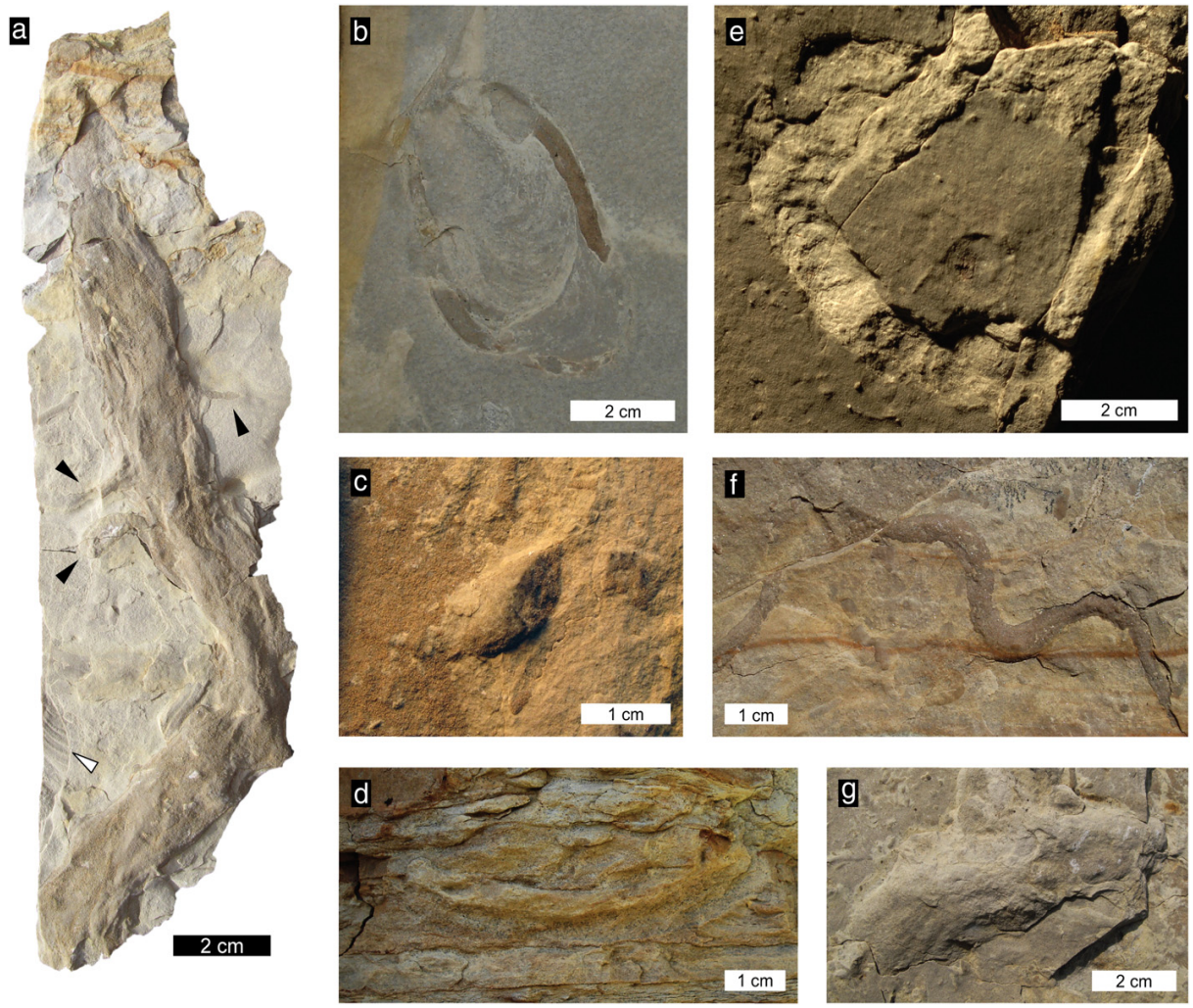

Fig. 4. Trace fossils from the lower Seis/Siusi Member from the Rosengarten/Catinaccio section. a: A single specimen of *Spongeliomorpha* isp. showing striations on the burrow wall and small branches (black arrows). White arrow points to a cast of *Claraia clarai* present (white arrow). b: Bedding plane with *Rhizocorallium* isp. c: *Lockeia* isp. on lower bedding plane. d: *Catenichnus contentus* in cross-sectional view. e: *Taenidium barretti* on upper bedding plane. f: *Helminthopsis* cf. *abeli* on upper bedding plane. g: cf. *Curvolithus* on lower bedding plane.

identical to host rock. False branching due to overlap of specimens may occur. Width ranges from 2 to 17 mm but is most commonly 4–7 mm.

Remarks. The most accepted ichnotaxonomic scheme for *Palaeophycus* is that of Pemberton and Frey (1982). They recommended assigning actively filled burrows to *Planolites* and passively filled burrows to *Palaeophycus*. However, Jensen (1997) noted that digested material may resemble the host sediment and passively introduced sediment may contrast with the host sediment. Another significant feature of *Palaeophycus* is the presence of wall linings (Pemberton and Frey, 1982; Keighley and Pickerill, 1995). *Palaeophycus tubularis* is distinguished from other ichnospecies of *Palaeophycus* by a thin lining and the absence of striations.

Palaeophycus is interpreted as a dwelling burrow of suspension-feeding or predatory worms (Pemberton and Frey, 1982). The ichnogenus is common in virtually all terrestrial and sub-aquatic environments (Pemberton and Frey, 1982), and ranges in age from Ediacaran (e.g., Seilacher et al., 2005) to Holocene (e.g., Gingras et al., 2008). *Palaeophycus* has also been reported from the Seis/Siusi Member by Twitchett and Wignall (1996).

3.2.6. *Planolites montanus* Richter, 1937

Material. Approximately 60 specimens observed in the field (Fig. 3a), Rosengarten section.

Description. Indistinct, sub-cylindrical to cylindrical, horizontal burrows with smooth surface. Predominantly preserved as full-reliefs. Burrow diameter ranges from less than 1 mm to 6 mm but is typically about 2 mm. Burrow fill darker than host rock.

Remarks. Planolites montanus is distinguished from other ichnospecies of *Planolites* by its small size, tortuous course, penetrative nature and lack of ornamentation (Pemberton and Frey, 1982). *Planolites* most likely reflects the activity of infaunal deposit-feeding, vermiform organisms, most likely polychaetes (Pemberton and Frey, 1982). *Planolites* is a facies-crossing ichnotaxon which has been documented from all marine and continental environments (Pemberton and Frey, 1982). It ranges in age from the latest Neoproterozoic (e.g. Narbonne and Hofmann, 1987) to the Pleistocene (e.g. Pemberton and Jones, 1988). *Planolites* has been previously reported from the Seis/Siusi Member by Twitchett and Wignall (1996).

3.2.7. Rhizocorallium isp.

Material. 5 specimens observed in the field (Fig. 4b), Rosengarten section.

Description. Horizontal U-shaped burrow with spreiten-structures between the arms. Diameter of arms is ca. 6 mm. In one case (Fig. 3a), an oblique array of retrusive spreiten is observed only.

Remarks. In contrast to other U-shaped burrows (*Arenicolites*, *Diplocraterion*) *Rhizocorallium* is characterized by its horizontal to oblique orientation. The material found in the Seis/Siusi Member is too poorly preserved to assign it to an ichnospecies of *Rhizocorallium*. The ichnogenus is interpreted as a suspension- and deposit-feeding burrow, most likely of crustaceans (Fürsich, 1974b). *Rhizocorallium* is most common in shallow-marine deposits (Fürsich, 1974b) but is reported from various settings including deep-marine (e.g. Uchman, 1991) marginal-marine (e.g. Hakes, 1976) and non-marine (e.g. Fürsich and Mayr, 1981). It ranges in age from Cambrian (Seilacher, 1955) to Miocene (Fürsich and Mayr, 1981). In the Werfen Formation, *Rhizocorallium* has previously been reported from the Spathian San Lucano Member (Twitchett and Wignall, 1996).

3.2.8. Spongeliomorpha isp.

Material. One specimen observed in the field (Fig. 4a), Rosengarten section.

Description. Subcylindrical, horizontal burrow with irregular, longitudinal striae. Burrow width is ca. 21 mm. The preserved burrow is more than 20 cm long and follows an irregular course. The burrow displays short branching segments, which diverge almost perpendicular from the main structure. Branches are straight and 2 mm to 4 mm wide. One branching segment is tear-shaped, increasing in diameter towards its terminal end.

Remarks. Because of their similar general morphology and the tendency to show intergradational stages, *Thalassinoides*, *Ophiomorpha*, and *Spongeliomorpha* were suggested to be synonymous (Fürsich, 1973b). However, this approach did not find general agreement among ichnologists (e.g. Bromley and Frey, 1974) because distinctive features of the burrow wall (smooth, ornamented or pelletal lining) were suggested to reflect significant behavioral differences and not only differential preservation of the same trace fossil. However, this view has been criticized by Schlirf (2000), who suggested to follow the revision of Fürsich (1973b). It is beyond the scope of this study to contribute to this debate. We follow the more established scheme and retain these forms as ichnotaxonomically distinct. The specimen of the Seis/Siusi Member is incomplete and, thus, ichnogeneric identification is difficult. However, the presence of small branched segments ending in blind tunnels (Gibert and Ekdale, 2010) and the striation justifies the assignation to *Spongeliomorpha*. The striation on the observed specimen is poorly developed and may be the result of compaction leading to a wrinkled burrow surface. *Spongeliomorpha* represents a deposit-feeding and dwelling burrow produced by crustaceans (Bromley, 1967) and is most common in shallow-marine environments (Schlirf, 2000).

3.2.9. Taenidium barretti (Bradshaw, 1981)

Material. One specimen (Fig. 4e), Rosengarten section.

Description. Horizontal burrow with meniscate backfill. Burrow diameter is 11 mm. Burrow course is highly irregular and secondary branching occurs. Internal meniscate lamination is rather poorly preserved.

Remarks. We follow the revision of meniscate backfilled burrows provided by Keighley and Pickerill (1994) who assigned the trace fossil originally erected as *Beaconites barretti* (Bradshaw, 1981) to *Taenidium*. The specimen from the Seis/Siusi Member readily corresponds to the diagnosis provided by Keighley and Pickerill (1994) and the slightly emended diagnosis in Schlirf (2000).

Taenidium is interpreted as deposit-feeding structure (Squires and Advocate, 1984) of worm-like animals (Schlirf, 2000). It is a facies-crossing form (Keighley and Pickerill, 1994 and references therein). *T. barretti* seems to be more common in terrestrial environments (Keighley and Pickerill, 1994) but it is also reported from shallow-marine deposits (Schlirf, 2000). The ichnogenus ranges in age from the Silurian (Dam and Andreasen, 1990) to the Pleistocene (D'Alessandro et al., 1992).

3.2.10. Thalassinoides cf. suevicus (Rieth, 1932)

Material. Approximately 20 specimens observed in the field (Fig. 3b–d), Rosengarten and Aferer Geisler section.

Description. Horizontal, sub-cylindrical systems of irregular, smooth burrows with mostly dichotomous, Y-shaped branchings. Swellings at the sites of branching are frequently observed. Burrow diameter ranges from 6 mm to 25 mm but is typically about 11 mm. These burrows are preserved as full-relief structures.

Remarks. The difficulties regarding the taxonomy of *Spongeliomorpha* and *Thalassinoides* are outlined in the discussion on *Spongeliomorpha*.

The specimens from the Seis/Siusi Member are composed of horizontal burrow systems with mainly dichotomous bifurcations showing slightly increased diameters at the sites of branchings. Thus, they largely correspond to the diagnosis of *Thalassinoides suevicus* (*Spongeliomorpha suevicus* of Fürsich, 1973a and Schlirf, 2000). However, large bedding planes (>m^2), providing observations of extended burrow systems were not available and the ichnospecies identification is therefore tentative.

Thalassinoides is interpreted as a deposit-feeding and dwelling burrow of crustaceans (Fürsich, 1973c). It represents a facies-crossing ichnotaxon being reported from deep-marine (Uchman, 1995) and, more commonly, shallow-marine environments (Fürsich, 1973a;Schlirf, 2000). The presumably oldest *Thalassinoides* has been described from the Cambrian (Sprechmann et al., 2004). Modern burrows produced by a multitude of different crustacean taxa correspond to the morphology of *Thalassinoides* (Bromley, 1996).

3.3. The recovery from an ichnological perspective

According to Twitchett and Wignall (1996), *Thalassinoides*, *Spongeliomorpha*, and *Rhizocorallium* were not documented from the Early Triassic recovery interval until Spathian times (late Early Triassic). However, later reports from mid and high latitude settings of western Pangaea (Wignall et al., 1998; Beatty et al., 2008; Zonneveld et al., 2010) have shown that some of these key ichnotaxa returned much earlier after the extinction, i.e. during Griesbachian times. This distribution in time and space has been interpreted as a latitudinally controlled signal indicating faster recovery in the Boreal Realm than in tropical regions (Twitchett and Barras, 2004). Furthermore, an explanatory model referred to as “habitable zone concept” has been proposed (Beatty et al., 2008) to align these data with the hypothesis that low-oxygen stress was a major cause of the delayed recovery (Wignall and Twitchett, 1996). In this model, Beatty et al. (2008) propose an optimum zone near the shoreface–offshore transition, which is characterized by sufficient oxygenation promoted by storms and by a high preservation potential because of negligible effects of fair-weather waves.

Data from the eastern Pangaean margin, particularly the occurrence of *Rhizocorallium* in Griesbachian rocks of the low-latitude Dinwoody Formation of the southwestern U.S. (Pruss and Bottjer, 2004; Fraiser and Bottjer, 2009) have partially challenged the concept of a delayed reappearance of those ichnotaxa that represent permanent dwelling and feeding burrows, and have also lessened assumed differences in the pace of the recovery between low and high latitudes. Furthermore, Fraiser and Bottjer (2009) noted that neither a gradual trend in diversity and burrow size is observed throughout the Early Triassic nor do certain trace fossils reappear in a strict succession on a global scale. Our data now demonstrate that a comparably diverse ichnofauna including key ichnotaxa was present in the Tethyan palaeo-tropics during the (late) Griesbachian as well, indicating an interregional late Griesbachian recovery of trace makers.

3.4. State of recovery

An informal definition of recovery stages has been presented by Twitchett (1999), based on the reappearances of ichnotaxa, tiering, and diversity from the Lower Triassic Werfen Formation. Later, Twitchett et al. (2004) presented an improved scheme suggesting four recovery stages based on quantifiable criteria such as burrow size, tiering, and diversity. Twitchett (2006) further extended the recovery scheme with defined recovery stages in order to quantify and compare recovery stages among different regions and different events. This scheme (Fig. 3 in Twitchett, 2006) incorporates several key features of benthic ecosystems: (1) tiering levels, (2) the presence/absence of key ichnotaxa, (3) body (or burrow) size, and (4) dominance and evenness of shelly assemblages. Twitchett (2006) noted that diversity and evenness of body fossil faunas are easily altered by preservational and taphonomic processes and therefore should be applied with some caution. Trace fossils are, however, considered as a reliable indicator of relative recovery stages. Twitchett (2006) and numerous recent studies (Pruss and Bottjer, 2004; Beatty et al., 2008; Fraiser and Bottjer, 2009; Knaust, 2010; Zonneveld et al., 2010; Chen et al., 2011) highlight the importance of the ichnologic approach to recognize recovery stages. The model of Twitchett (2006) provides several parameters to gage biotic recovery but most field studies can rely on some aspects only, depending on the availability and nature of data. For instance, Twitchett et al. (2004) defined a recovery stage of 3 for a Griesbachian fauna from Oman exclusively based on shelly fossils. Conversely, high recovery ichnofaunas from the Boreal Realm yield no information on body fossils.

Following the model of Twitchett (2006), the ichnofauna of the lower Seis/Siusi Member (Fig. 5b) corresponds roughly to a recovery stage of 3 to 4. Key ichnotaxa (*Thalassinoides*, *Rhizocorallium*), characteristic for stages 3 and 4, are present and some burrows exceed 20 mm in diameter (typical for stage 4). Associated body fossils (e.g. *Claraia clarai*), recorded in intercalated limestone beds do not show a notably reduced body size (39 mm in diameter on mean average). Tiering in the lower Seis/Siusi fauna is still relatively simple (Fig. 5b) and erect, epifaunal forms (e.g. crinoids) are not recorded. However, the absence of body fossils in intervals that are rich in ichnofossils can be misleading and crinoids are not reported from "high recovery" ichnofaunas elsewhere (Beatty et al., 2008; Zonneveld et al., 2010).

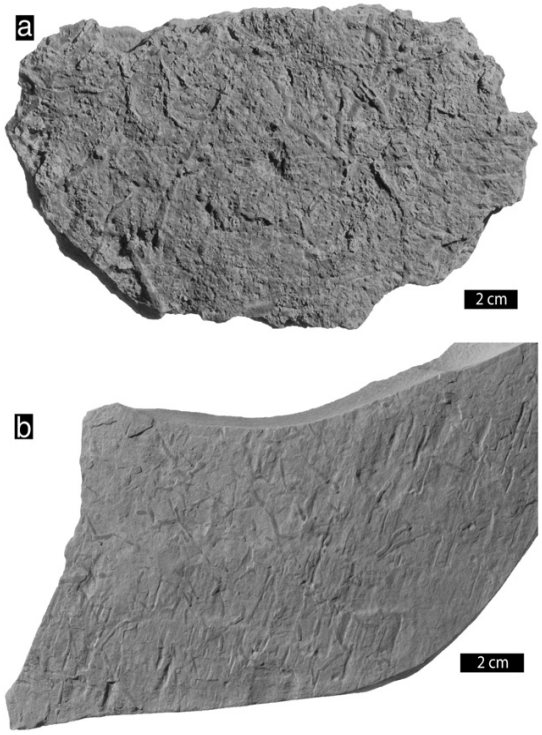

Fig. 6. Trace fossils from the Mazzin Member at the Aferer Geisler locality a: *Planolites montanus* b: cf. *Chondrites*.

The trace fossils occur in a transgressive interval above the supratidal deposits of the Andraz Member (Broglio Loriga et al., 1983; Twitchett and Wignall, 1996). This abrupt facies change may mask a more gradual recovery of trace fossil communities than reflected by their sudden appearance. However, the lower and middle parts of the underlying Mazzin Member record the same range of water depth and a similar sedimentary facies (Broglio Loriga et al., 1983; own observation) as in the lower Seis Member but lack "complex" trace fossil assemblages. Instead, bioturbation in these parts of the Mazzin Member is restricted

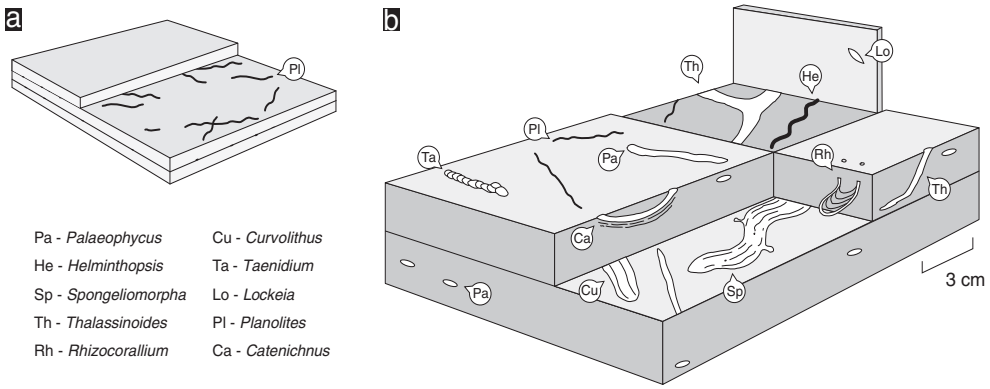

Fig. 5. Ichnofaunas from the lower Werfen Formation. a: Mazzin Member. b: Lower Seis/Siusi Member.

to a few horizons with *Planolites*-type burrows (Figs. 5a, 6a) and one poorly preserved burrow system which could be tentatively assigned to *Chondrites* (Fig. 6b). The small burrow diameter, low diversity and very shallow tiering suggest recovery stage 1 (*sensu* Twitchett, 2006) for virtually the entire Mazzin Member.

We consider the ichnofauna of the Seis/Siusi Member to record a genuine recovery signal of trace makers, which reflects the return of infaunal crustaceans and complex metazoan behavior in shallow-marine benthic communities of the western equatorial Tethys. In the remaining part of the Seis/Siusi Member, recognizable bioturbation decreases and returns to low levels, very likely as the result of the shallowing-upward trend and of wave reworking and facies restriction (Broglio Loriga et al., 1983; Twitchett, 1999). Ichnogenera reported from the late Permian Bellerophon Formation include *Zoophycos*, *Rhizocorallium*, *Skolithos*, *Diplocraterion* and *Planolites* (Twitchett, 1999). Except for *Zoophycus*, these trace fossils occur in the Seis/Siusi Member (Twitchett, 1999; this study). Accordingly, most types of metazoan behavior present before the extinction became reestablished in the course of Griesbachian and Dienerian times, at least temporarily. The absence of *Zoophycos* does not diminish the significance of the Seis/Siusi ichnofauna because it is not recorded in Lower Triassic strata worldwide (Fraiser and Bottjer, 2009) and it first reappears in the Middle Triassic (Knaust, 2004).

4. Discussion

The traditional perspective on the recovery interval suggests that long-lasting, harsh environmental conditions have played the major role in inhibiting the recovery of benthic communities for most of the Early Triassic (Hallam, 1991; Wignall and Twitchett, 1996). In particular, the view that persistent shallow-marine anoxia was a key factor in inhibiting the rediversification of benthic organisms (Wignall and Hallam, 1992; Wignall and Twitchett, 1996) was adopted until most recent studies (e.g. Zonneveld et al., 2010). Based on the analysis of Th/U ratios of deposits from low-latitude settings and sedimentological studies from mid-latitudes, it has been suggested that widespread anoxic conditions, extending in shallow waters, prevailed during most of the Griesbachian but waned quite rapidly at the end of this stage (Wignall and Twitchett, 1996). Our finding of a diverse ichnofauna in the initial "non-anoxic" interval at one of the field sites studied by Wignall and Twitchett (1996) seems to be in accordance with this scenario because marine trace fossils related to crustaceans, as described herein, usually indicate normal marine oxygenation (Bromley and Ekdale, 1984; Savrda and Bottjer, 1986). An *ad-hoc* interpretation of this pattern is that localities devoid of anoxia in shallow-marine environments (e.g. Wignall et al., 1998; Krystyn et al., 2003; Wignall and Newton, 2003; Twitchett et al., 2004; Beatty et al., 2008; Knaust, 2010;) served as refuges for biota that subsequently recolonized other regions as soon as the environmental conditions improved.

Although the trace fossil distribution reported herein has no decisive implications with respect to the anoxia scenario mentioned above, we note that also reduced biogenic mixing, as a consequence of the extinction of burrowing taxa, could have produced much of the phenomena such as low Th/U ratios, frequent pyrite, and sediment lamination that have previously been ascribed to seawater anoxia by Wignall and Twitchett (1996). This mechanism has been already invoked by Erwin (1993, p 246) but has scarcely been considered in subsequent studies. Furthermore, dysoxic to anoxic conditions recorded in the Ceratite Marls of the Mittiwali Member (Salt Range, Pakistan) were incorrectly assigned to the Griesbachian by Wignall and Hallam (1993). As shown by Hermann et al. (2011a), dysoxic to anoxic conditions in the Early Triassic of the Salt Range were actually restricted to the Dienerian. In addition, Ware et al. (2011) documented that oxygen-restriction on the Induan shelf of the Western U.S. (Candelaria Formation, Nevada) is apparently confined to strata younger than latest Griesbachian or most likely Early Dienerian.

Thus, alternative scenarios with an emphasis on other kinds of environmental stress that may have persisted into the Early Triassic cannot be ruled out as an explanation for the observed recovery signal. Such environmental stress may have been elevated atmospheric CO_2-levels (Fraiser and Bottjer, 2007; Payne et al., 2007), fluctuations of seawater pH-values (Payne et al., 2007), SO_2 and halocarbon emissions (Svensen et al., 2009), or intrinsic traits of recovery dynamics. Besides the trace fossil rebound shown herein,

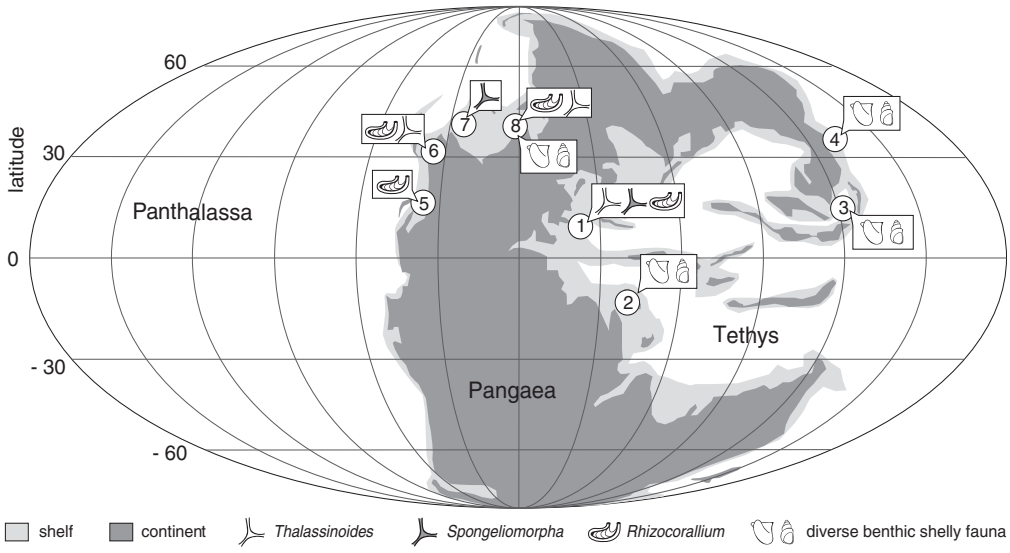

Fig. 7. Distribution of Griesbachian and some Dienerian ichnofaunas and shelly faunas that reflect advanced recovery stages (at least recovery stage 3 *sensu* Twitchett, 2006). 1: Italy, Griesbachian, key ichnotaxa present, high ichnodiversity, (this study; Twitchett and Wignall, 1996), 2: Oman, Griesbachian, 14 benthic mollusc genera (Twitchett et al., 2004), 3: South China, Griesbachian, 15 benthic mollusc species (Kaim et al., 2010; Hautmann et al., 2011), 4: Primorye, Griesbachian, 15 benthic mollusc species (Shigeta et al., 2009), 5: Western U.S., Griesbachian, key ichnotaxa present (Fraiser and Bottjer, 2009), 6: British Columbia, Griesbachian, key ichnotaxa present, high ichnodiversity (Beatty et al., 2008 and references therein), 7: Nunavut, Griesbachian, key ichnotaxa present, high ichnodiversity (Beatty et al., 2008 and references therein), 8. Svalbard, Griesbachian and Early Dienerian, key ichnotaxa present, high ichnodiversity, comparatively diverse shelly fauna (Wignall et al., 1998). Palaeogeographic restoration after Blakey (2011).

recent analyses of body fossil faunas from Oman (Krystyn et al., 2003), far-east Russia (Shigeta et al., 2009) and China (Kaim et al., 2010; Hautmann et al., 2011) suggest that advanced recovery stages of benthic ecosystems during the Griesbachian were not restricted to some refuges of the Boreal ocean or some oxygenated zones of the Tethys (Fig. 7). Another shelly fauna of probable Griesbachian age has been mentioned from Selong (southern Tibet; Wignall and Newton, 2003) but is here excluded from the discussion because this section has probably been affected by condensation, gaps and time averaging (MH, pers. observations). The increasing number of studies that report "advanced" recovery faunas (*sensu* Twitchett et al., 2004) from the late Griesbachian worldwide (Fig. 7) challenges the generalized concept of protracted and gradual recovery of the benthos during the Early Triassic (e.g. Hallam, 1991; Wignall and Hallam, 1992; Twitchett 1999; Pruss and Bottjer, 2004; Twitchett and Barras, 2004; Fraiser and Bottjer, 2005; Bottjer et al., 2008). Following the recently established geochronological framework (Ovtcharova et al., 2006; Galfetti et al., 2007), the data presented herein together with those from the recent literature show that advanced restoration of benthic ecosystems on a global scale (Fig. 7) must have been underway only some 0.5 million - years after the main extinction phase.

Ecological structure of ichnofaunas apparently returned to less "advanced" stages later in the Early Triassic of the Werfen Formation (Fig. 8) (Twitchett and Wignall, 1996; own observations). Intervals

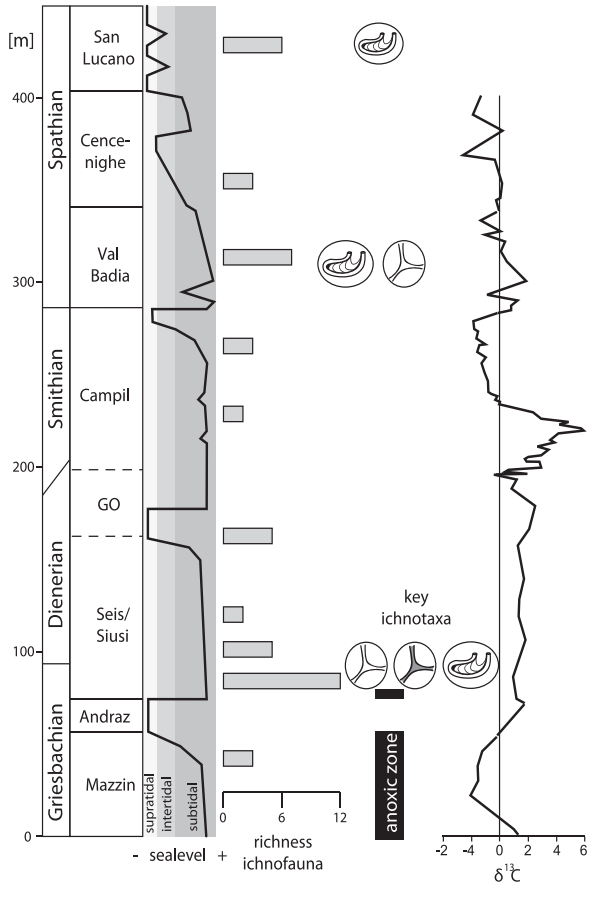

Fig. 8. Ichnodiversity throughout the Werfen Formation (approximate thickness after Twitchett and Wignall, 1996) indicated by the number of ichnogenera (after Twitchett and Wignall, 1996; this study). Sea level curve after Broglio Loriga et al. (1983) and carbon isotope curve after Horacek et al. (2007). The presence of ichnogenera with high recovery significance is specified within each bar (for trace fossil key see Fig. 7). The position of the "anoxic zone" is after Wignall and Twitchett (1996). GO — gastropod oolite.

where subtidal conditions are recorded should contain comparable ichnofossil assemblages (*Cruziana* ichnofacies *sensu lato*) in behavioral and ichnotaxonomic complexity. This applies only to the lower Seis/Siusi and the Val Badia Member. The Campil Member may record local stress factors including high siliciclastic input and concurrent changes in salinity (Twitchett and Wignall, 1996). However, large fluctuations of the $\delta^{13}C$ reflecting global perturbations roughly correspond with low-diverse trace fossil assemblages (Fig. 8). Smithian trace fossil data from other localities such as the western U.S. (Pruss and Bottjer, 2004; Fraiser and Bottjer, 2009) and China (Chen et al., 2011) are relatively simple, which could point to a global phenomenon. Similarly, benthic shelly faunas from the western U.S. are not much diverse throughout the Early Triassic (Schubert and Bottjer, 1995), with the exclusion of the Spathian (McGowan et al., 2009; own data). This pattern indicates that the general restoration of benthic ecosystems was markedly slowed down or reset in later, post-Griesbachian times. In fact, Fraiser and Bottjer (2009) hypothesized that benthic ecosystems may have been subjected to repeated rather than persistent adverse environmental conditions.

Post P-T extinction crises have been confidently identified in nektonic groups such as ammonoids and conodonts (Brayard et al., 2006; Ovtcharova et al., 2006; Orchard, 2007) but have previously not been unequivocally recognized in benthic biota. Stanley (2009) speculated that benthic ecosystems may show a recovery pattern that is in accordance with a multiple extinction scenario. Currently, it is poorly understood whether the mechanisms that caused Early Triassic extinctions of nektonic biota or the possible repeated demises of terrestrial ecosystems (Hochuli et al., 2010; Retallack et al., 2011) and floral turnovers (Hermann et al., 2011b) affected benthic clades to a similar extent and timing, and further research is necessary to pin down environmental constraints on post-Griesbachian setbacks. However, the general pattern with early recovery pulses that were repeatedly set back by deteriorating environmental conditions is readily applicable to benthic ecosystems. This multiple crises model provides an alternative interpretation of the Early Triassic history of benthic biodiversity, which challenges the widely held and classic assumptions that (i) persistent catastrophic conditions in the early aftermath of the extinction were the key factor in delaying the recovery of marine benthos or that (ii) the extreme intensity of the end-Permian extinction led to a proportionate duration in the reengineering of ecological networks (Schubert and Bottjer, 1995; Erwin, 2001).

5. Conclusions

The new data presented herein and the distribution of known trace fossil occurrences strongly suggest a significant global recovery of benthic ecosystems fairly soon after the most severe mass extinction in the history of metazoan life. The recovery apparently proceeded at a comparable pace across low and high palaeo-latitudes and ichnofaunas comprising several key ichnotaxa (*Thalassinoides*, *Rhizocorallium*, and *Spongeliomorpha*) were not restricted to "refuges". The re-evaluation of the overall recovery pattern indicates that the apparently sluggish recovery of benthic organisms probably reflects multiple setbacks during the Early Triassic rather than persistent environmental disturbances in the early aftermath of the extinction.

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References

Beatty, T.W., Zonneveld, J.P., Henderson, C.M., 2008. Anomalously diverse Early Triassic ichnofossil assemblages in Northwest Pangea: a case for a shallow-marine habitable zone. Geology 36, 771–774.

Blakey, R., 2011. Global Paleogeography. http://www2.nau.edu/rcb7/globaltext2.html (2011).

Bottjer, D.J., Clapham, M.E., Frasier, M.L., Powers, C.M., 2008. Understanding mechanisms for the end-Permian mass extinction and the protracted Early Triassic aftermath and recovery. GSA Today 18, 4–10.

Bradshaw, M.A., 1981. Paleoenvironmental interpretations and systematics of Devonian trace fossils from the Taylor Group (lower Beacon Supergroup), Antarctica. NZ J. Geol. Geophys 24, 615–652.

Brayard, A., Bucher, H., Escarguell, G., Fluteau, F., Bourquin, S., Galfetti, T., 2006. The Early Triassic ammonoid recovery: paleoclimatic significance of diversity gradients. Palaeogeogr. Palaeoclimatol. Palaeoecol. 239, 374–395.

Brayard, A., Escarguell, G., Bucher, H., Monnet, C., Brühwiler, T., Goudemand, N., Galfetti, T., Guex, J., 2009. Good genes and good luck: ammonoid diversity and the end-Permian mass extinction. Science 325, 1118–1121.

Broglio Loriga, C., Masetti, D., Neri, C., 1983. La Formazione di Werfen (Scitico) delle Dolomiti occidentali: Sedimentologia e biostratigrafia. Riv. Ital. Pal. Strat. 58, 501–598.

Bromley, R.G., 1967. Some observations on burrows of Thalassinidean Crustacea in chalk hardgrounds. Q. J. geol. Soc. 123, 157–177.

Bromley, R.G., 1996. Trace Fossils: Biology, Taphonomy and Applications, 2nd Edition. Chapman & Hall, London. 361 pp.

Bromley, R.G., Ekdale, A.A., 1984. *Chondrites* — a trace fossil indicator of anoxia in sediments. Science 224, 872–874.

Bromley, R.G., Frey, R.W., 1974. Redescription of the trace fossil *Gyrolithes* and taxonomic evaluation of *Thalassinoides*, *Ophiomorpha* and *Spongeliomorpha*. Bull. Geol. Soc. Den. 23, 311–335.

Buatois, L.A., Mangano, M.G., Maples, C.G., Lanier, W.P., 1998a. Ichnology of an Upper Carboniferous fluvio-estuarine paleovalley: the Tonganoxie Sandstone, Buildex Quarry, Eastern Kansas, USA. J. Paleontol. 72, 152–180.

Buatois, L.A., Mangano, G., Mikulas, R., Maples, C.G., 1998b. The ichnogenus *Curvolithus* revisited. J. Paleontol. 72, 758–769.

Chen, Z.-Q., Tong, J., Fraiser, M.L., 2011. Trace fossil evidence for restoration of marine ecosystems following the end-Permian mass extinction in the Lower Yangtze region, South China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 299, 449–474.

D'Alessandro, A., Loiacono, F., Bromley, R.G., 1992. Marine and nonmarine trace fossils and plant roots in a regressional setting (Pleistocene, Italy). Riv. Ital. Pal. Strat. 98, 495–522.

Dam, G., Andreasen, F., 1990. High-energy ephemeral stream deltas — an example from the Upper Silurian Holmestrand Formation of the Oslo Region, Norway. Sediment. Geol. 66, 197–225.

Droser, M.L., Bottjer, D.J., 1986. A semiquantitative field classification of ichnofabric. J. Sediment. Petrol. 56, 558–559.

Enos, P., 1983. Shelf environment. In: Scholle, P.A., Bebout, D.G., Moore, C.H. (Eds.), Carbonate Depositional Environments. American Association of Petroleum Geologists, Tulsa, Oklahoma, pp. 268–295.

Erwin, D.H., 1993. The Great Paleozoic Crisis: Life and Death in the Permian. Critical Moments in Paleobiology and Earth History Series. Columbia University Press, New York. 327 pp.

Erwin, D.H., 2001. Lessons from the past: biotic recoveries from mass extinctions. Proc. Natl Acad. Sci. USA 98, 5399–5403.

Fillion, D., Pickerill, R.K., 1990. Ichnology of the Upper Cambrian? to Lower Ordovician Bell Island and Wabana groups of eastern Newfoundland. Palaeontogr. Canadiana 7 119 pp.

Fraiser, M.L., Bottjer, D.J., 2005. Restructuring in benthic level-bottom shallow marine communities due to prolonged environmental stress following the end-Permian mass extinction. CR Palevol 4, 583–591.

Fraiser, M.L., Bottjer, D.J., 2007. Elevated atmospheric CO2 and the delayed biotic recovery from the end-Permian mass extinction. Palaeogeogr. Palaeoclimatol. Palaeoecol. 252, 164–175.

Fraiser, M.L., Bottjer, D.J., 2009. Opportunistic behaviour of invertebrate marine tracemakers during the Early Triassic aftermath of the end-Permian mass extinction. Aust. J. Earth Sci. 56, 841–857.

Fürsich, F.T., 1973a. Corallian (Upper Jurassic) trace fossils from England and Normandy. Stuttgarter Beiträge zur Naturkunde 13, 1–52 Serie B.

Fürsich, F.T., 1973b. *Thalassinoides* and the origin of nodular limestone in the Corallian beds (Upper Jurrasic) of Southern England. Neues Jb Geol. Paläontol. Monatsh. 3, 136–156.

Fürsich, F.T., 1973c. A revision of the trace fossils *Spongeliomorpha*, *Ophiomorpha* and *Thalassinoides*. Neues Jb Geol. Paläontol. Monatsh. 12, 719–735.

Fürsich, F.T., 1974a. *Diplocraterion* Torell 1870 and significance of morphological features in vertical, spreiten-bearing, U-shaped trace fossils. J. Paleontol. 48, 952–962.

Fürsich, F.T., 1974b. Ichnogenus *Rhizocorallium*. Paläontol. Z. 48, 16–28.

Fürsich, F.T., Mayr, H., 1981. Non-marine *Rhizocorallium* (trace fossil) from the Upper Freshwater Molasse (Upper Miocene) of southern Germany. Neues Jb Geol. Paläontol. Monatsh. 6, 321–333.

Galfetti, T., Bucher, H., Ovtcharova, M., Schaltegger, U., Brayard, A., Brühwiler, T., Goudemand, N., Weissert, H., Hochuli, P.A., Cordey, C., Guodun, K., 2007. Timing of the Early Triassic carbon cycle perturbations inferred from new U–Pb ages and ammonoid biochronozones. Earth Planet. Sci. Lett. 258, 593–604.

Gibert, J.M.d., Ekdale, A.A., 2010. Paleobiology of the crustacean trace fossil *Spongeliomorpha iberica* in the Miocene of southeastern Spain. Acta Palaeontol. Pol 55, 733–740.

Gibson, G.G., 1989. Trace fossils from Late Precambrian Carolina Slate Belt, South-Central North-Carolina. J. Paleontol. 63, 1–10.

Gingras, M.K., Dashtgard, S.E., MacEachern, J.A., Pemberton, S.G., 2008. Biology of shallow marine ichnology: a modern perspective. Aqu. Biol. 2, 255–268.

Hakes, W.G., 1976. Trace fossils and depositional environment of four clastic units, Upper Pennsylvanian megacyclothems, northeast Kansas. University of Kansas paleontological contributions: Article, vol. 63, pp. 1–6.

Hall, J., 1847. Natural history of New York. Palæontology of New York, Vol. I. 1. Van Benthuysen, Albany, NY. 338 pp.

Hallam, A., 1991. Why was there a delayed radiation after the end-Palaeozoic extinctions? Hist. Biol. 5, 257–262.

Hautmann, M., Bucher, H., Brühwiler, T., Goudemand, N., Kaim, A., Nützel, A., 2011. An unusually diverse mollusc fauna from the earliest Triassic of South China and its implications for benthic recovery after the end-Permian biotic crisis. Geobios 44, 71–85.

Hermann, E., Hochuli, P.A., Méhay, S., Bucher, H., Brühwiler, T., Hautmann, M., Ware, D., Roohi, G., Ur-Frehman, K., Yaseen, A., 2011a. Organic matter and palaeoenvironmental signals during the Early Triassic biotic recovery: the Salt Range and Surghar Range records. Sediment. Geol. 234, 19–41.

Hermann, E., Hochuli, P.A., Bucher, H., Brühwiler, T., Hautmann, M., Ware, D., Roohi, G., 2011b. Terrestrial ecosystems on North Gondwana following the end-Permian mass extinction. Gondwana Res. 20, 630–637.

Hochuli, P.A., Hermann, E., Vigran, J.O., Bucher, H., Weissert, H., 2010. Rapid demise and recovery of plant ecosystems across the end-Permian extinction event. Global Planet. Change 74, 144–155.

Horacek, M., Brandner, R., Abart, R., 2007. Carbon isotope record of the P/T boundary and the Lower Triassic in the Southern Alps: evidence for rapid changes in storage of organic carbon. Palaeogeogr. Palaeoclimatol. Palaeoecol. 252, 347–354.

Jensen, S., 1997. Trace fossils from the Lower Mickwitzia sandstone, south-central Sweden. Fossils Strata 42, 1–110.

Kaim, A., Nutzel, A., Bucher, H., Brühwiler, T., Goudemand, N., 2010. Early Triassic (Late Griesbachian) gastropods from South China (Shanggan, Guangxi). Swiss J. Geosci. 103, 121–128.

Keighley, D.G., Pickerill, R.K., 1994. The ichnogenus *Beaconites* and its distinction from *Ancorichnus* and *Taenidium*. Palaeontology 37, 305–337.

Keighley, D.G., Pickerill, R.K., 1995. The ichnotaxa *Palaeophycus* and *Planolites*: historical perspectives and recommendations. Ichnos 3, 301–309.

Keij, A., 1965. Miocene trace fossils from Borneo. Paläontol. Z. 39, 220–228.

Knaust, D., 2004. The oldest Mesozoic nearshore *Zoophycos*: evidence from the German Triassic. Lethaia 37, 297–306.

Knaust, D., 2010. The end-Permian mass extinction and its aftermath on an equatorial carbonate platform: insights from ichnology. Terra Nova 22, 195–202.

Krystyn, L., Richoz, S., Baud, A., Twitchett, R.J., 2003. A unique Permian–Triassic boundary section from the Neotethyan Hawasina Basin, Central Oman Mountains. Palaeogeogr. Palaeoclimatol. Palaeoecol. 191, 329–344.

Książkiewicz, M., 1977. Trace fossils in the Flysch of the Polish Carpathians. Palaeontol. Pol. 36 208 pp..

Mángano, M.G., Buatois, L.A., West, R.R., Maples, C.G., 2002. Ichnology of a Pennsylvanian equatorial tidal flat — the Stull Shale Member at Waverly, eastern Kansas. Kansas Geological Survey Bulletin, vol. 245. Lawrance, Kansas. 133 pp.

Mccarthy, B., 1979. Trace fossils from a Permian shoreface–foreshore environment, Eastern Australia. J. Paleontol. 53, 345–366.

McGowan, A.J., Smith, A.B., Taylor, P.D., 2009. Faunal diversity, heterogeneity and body size in the Early Triassic: testing post-extinction paradigms in the Virgin Limestone of Utah, USA. Aust. J. Earth Sci. 56, 859–872.

Mcllroy, D., 2004. Some ichnological concepts, methodologies, applications and frontiers. In: Mcllroy, D. (Ed.), Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis: Geological Society of London, Special Publication No. 228, pp. 3–27.

Miller, M.F., Smail, S.E., 1997. A semiquantitative field method for evaluating bioturbation on bedding planes. Palaios 12, 391–396.

Narbonne, G.M., Hofmann, H.J., 1987. Ediacaran Biota of the Wernecke Mountains, Yukon, Canada. Palaeontology 30, 647–676.

Orchard, M.J., 2007. Conodont diversity and evolution through the latest Permian and Early Triassic upheavals. Palaeogeogr. Palaeoclimatol. Palaeoecol. 252, 93–117.

Ovtcharova, M., Bucher, H., Schaltegger, U., Galfetti, T., Brayard, A., Guex, J., 2006. New Early to Middle Triassic U–Pb ages from South China: calibration with ammonoid biochronozones and implications for the timing of the Triassic biotic recovery. Earth Planet. Sci. Lett. 243, 463–475.

Payne, J.L., Lehrmann, D.J., Follett, D., Seibel, M., Kump, L.R., Riccardi, A., Altiner, D., Sano, H., Wei, J., 2007. Erosional truncation of uppermost Permian shallow-marine carbonates and implications for Permian–Triassic boundary events. Geol. Soc. Am. Bull. 119, 771–784.

Pemberton, S.G., Frey, R.W., 1982. Trace fossil nomenclature and the *Planolites–Palaeophycus* dilemma. J. Paleontol. 56, 843–881.

Pemberton, S.G., Jones, B., 1988. Ichnology of the Pleistocene Ironshore Formation, Grand Cayman Island, British West-Indies. J. Paleontol. 62, 495–505.

Péron, S., Bourquin, S., Fluteau, F., Guillocheau, F., 2005. Paleoenvironment reconstructions and climate simulations of the Early Triassic: impact of the water and sediment supply on the preservation of fluvial systems. Geodin. Acta 18, 431–446.

Posenato, R., 2008. Global correlations of mid Early Triassic events: the Induan/Olenekian boundary in the Dolomites (Italy). Earth Sci. Rev. 91, 93–105.

Pruss, S.B., Bottjer, D.J., 2004. Early Triassic trace fossils of the western United States and their implications for prolonged environmental stress from the end-Permian mass extinction. Palaios 19, 551–564.
Retallack, G.J., Sheldon, N.D., Carr, P.F., Fanning, M., Thompson, C.A., Williams, M.L., Jones, B.G., Hutton, A., 2011. Multiple Early Triassic greenhouse crises impeded recovery from Late Permian mass extinction. Palaeogeogr. Palaeoclimatol. Palaeoecol. 308, 233–251.
Richter, R., 1937. Marken und Spuren aus allen Zeiten. I–II. Senckenb. 19, 150–163.
Rieth, A., 1932. Neue Funde spongeliomorpher Fucoiden aus den Jura Schwabens. Geologische und Paläontologische Abhandlungen 19, 257–294.
Savrda, C.E., Bottjer, D.J., 1986. Trace-fossil model for reconstruction of paleo-oxygenation in bottom waters. Geology 14, 3–6.
Schlirf, M., 2000. Upper Jurassic trace fossils from the Boulonnais (northern France). Geol. Palaeontol. 34, 145–213.
Schubert, J.K., Bottjer, D.J., 1995. Aftermath of the Permian–Triassic Mass Extinction Event — paleoecology of Lower Triassic carbonates in the Western USA. Palaeogeogr. Palaeoclimatol. Palaeoecol. 116, 1–39.
Seilacher, A., 1953. Studien zur Palichnotogie II. Die fossilen Ruhespuren (Cubichnia). Neues Jb Geol. Paläontol. Abh. 98, 87–124.
Seilacher, A., 1955. Spuren und Fazies im Unterkambrium. In: Schindewolf, O.H., Seilacher, A. (Eds.), Beiträge zur Kenntnis des Kambriums in der Salt Range (Pakistan). Akademie der Wissenschaften und der Literatur in Mainz, Wiesbaden, pp. 11–143.
Seilacher, A., 1967. Bathymetry of trace fossils. Mar. Geol. 5, 413–428.
Seilacher, A., Buatois, L.A., Mangano, M.G., 2005. Trace fossils in the Ediacaran–Cambrian transition: behavioral diversification, ecological turnover and environmental shift. Palaeogeogr. Palaeoclimatol. Palaeoecol. 227, 323–356.
Shigeta, Y., Zakharov, Y.D.H.M., Popov, A.M. (Eds.), 2009. The Lower Triassic System in the Abrek Bay Area, South Primorye, Russia. National Museum of Nature and Science. 218 pp.
Sprechmann, P., Gaucher, C., Blanco, G., Montana, J., 2004. Stromatolitic and trace fossils community of the Cerro Victoria Formation, Arroyo del Soldado Group (Lowermost Cambrian, Uruguay). Gondwana Res. 7, 753–766.
Squires, R.L., Advocate, D.M., 1984. Meniscate burrows from Miocene lacustrine–fluvial deposits, Diligencia Formation, Orocopia Mountains, Southern-California. J. Paleontol. 58, 593–597.
Stanley, S.M., 2009. Evidence from ammonoids and conodonts for multiple Early Triassic mass extinctions. Proc. Natl Acad. Sci. USA 106, 15264–15267.
Svensen, H., Planke, S., Polozov, A.G., Schmidbauer, N., Corfu, F., Podladchikov, Y.Y., Jamtveit, B., 2009. Siberian gas venting and the end-Permian environmental crisis. Earth Planet. Sci. Lett. 277, 490–500.
Swinbanks, D.D., Murray, J.W., 1981. Biosedimentological zonation of Boundary Bay Tidal Flats, Fraser-River Delta, British-Columbia. Sedimentology 28, 201–237.
Twitchett, R.J., 1999. Palaeoenvironments and faunal recovery after the end-Permian mass extinction. Palaeogeogr. Palaeoclimatol. Palaeoecol. 154, 27–37.
Twitchett, R.J., 2006. The palaeoclimatology, palaeoecology and palaeo environmental analysis of mass extinction events. Palaeogeogr. Palaeoclimatol. Palaeoecol. 232, 190–213.
Twitchett, R.J., Barras, C.G., 2004. Trace fossils in the aftermath of mass extinction events. In: McIlroy, D. (Ed.), Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis: Geological Society of London, Special Publication No. 228, pp. 95–415.
Twitchett, R.J., Wignall, P.B., 1996. Trace fossils and the aftermath of the Permo-Triassic mass extinction: evidence from northern Italy. Palaeogeogr. Palaeoclimatol. Palaeoecol. 124, 137–151.
Twitchett, R.J., Krystyn, L., Baud, A., Wheeley, J.R., Richoz, S., 2004. Rapid marine recovery after the end-Permian mass-extinction event in the absence of marine anoxia. Geology 32, 805–808.
Uchman, A., 1991. Trace fossils from stress environments in Cretaceous–Palaeogene flysch of the Polish Outer Carpathians. Ann. Soc. Geol. Pol. 61, 207–220.
Uchman, A., 1995. Taxonomy and paleoecology of flysch trace fossils: the Marnoso–Arenacea Formation and associated facies (Northern Apennines, Italy). Beringeria 15, 3–115.
Ware, D., Jenks, J.F., Hautmann, M., Bucher, H., 2011. Dienerian (Early Triassic) ammonoids from the Candelaria Hills (Nevada, USA) and their significance for palaeobiogeography and palaeoceanography. Swiss J. Geosci. 104, 161–181.
Webby, B.D., 1970. Late Precambrian trace fossils from new south wales. Lethaia 3, 79–109.
Wetzel, A., Bromley, R.G., 1996. Re-evaluation of the ichnogenus *Helminthopsis* — a new look at the type material. Palaeontology 39, 1–19.
Wignall, P.B., Hallam, A., 1992. Anoxia as a cause of the Permian Triassic mass extinction — facies evidence from Northern Italy and the Western United-States. Palaeogeogr. Palaeoclimatol. Palaeoecol. 93, 21–46.
Wignall, P.B., Hallam, A., 1993. Griesbachian (Earliest Triassic) paleoenvironmental changes in the Salt Range, Pakistan and Southeast China and their bearing on the Permo-Triassic mass extinction. Palaeogeogr. Palaeoclimatol. Palaeoecol. 102, 215–237.
Wignall, P.B., Newton, R., 2003. Contrasting deep-water records from the Upper Permian and Lower Triassic of South Tibet and British Columbia: evidence for a diachronous mass extinction. Palaios 18, 153–167.
Wignall, P.B., Twitchett, R.J., 1996. Oceanic anoxia and the end Permian mass extinction. Science 272, 1155–1158.
Wignall, P.B., Morante, R., Newton, R., 1998. The Permo-Triassic transition in Spitsbergen: delta C-13(org) chemostratigraphy, Fe and S geochemistry, facies, fauna and trace fossils. Geol. Mag. 135, 47–62.
Zonneveld, J.-P., Gingras, M.K., Beatty, T.W., 2010. Diverse ichnofossil assemblages following the P–T mass extinction, Lower Triassic, Alberta and British Columbia, Canada: evidence for shallow marine refugia in the northwestern coast of Pangaea. Palaios 25, 368–392.

Chapter 2

Palaeoecology of the Spathian Virgin Formation (Utah, USA) and its implications for the Early Triassic recovery

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"Brothers, brothers! We should be struggling together!"

Brian in *Monty Python's Life of Brian* (1979)

Palaeoecology of the Spathian Virgin Formation (Utah, USA) and its implications for the Early Triassic recovery

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Hofmann, R., Hautmann, M., Wasmer, M., and Bucher, H. 2013. Palaeoecology of the Spathian Virgin Formation (Utah, USA) and its implications for the Early Triassic recovery. *Acta Palaeontologica Polonica* 58 (1): 149–173.

The Spathian (late Early Triassic) Virgin Formation of south-western Utah (USA) yields a comparatively diverse benthic fauna that flourished ~2 Ma after the end-Permian mass extinction. In this study, we present quantitative palaeoecological data, which are analysed in the context of depositional environments. This integrated approach helps to discriminate between effects of the end-Permian mass extinction event and local environmental factors on alpha diversity and ecological structure of the Virgin Fauna. Shallow subtidal environments yield the highest species richness and lowest dominance values as recorded in two benthic associations, the *Eumorphotis ericius* Association and the *Protogusarella smithi* Association, both of which contain 20 benthic species (bivalves, gastropods, brachiopods, echinoderms, and porifers). Tidal inlet deposits yield a low diverse fauna (*Piarorhynchella triassica* Association) with a very high dominance of filter feeders adapted to high energy conditions. Another comparably low diverse fauna is recorded by the *Bakevellia exporrecta* Association, which occurs in deposits of the offshore transition zone, most likely reflecting unconsolidated substrates. A single sample containing five bivalve species (*Bakevellia costata* Assemblage) is recorded from a marginal-marine setting. The Virgin fauna yields a bulk diversity of 30 benthic species (22 genera) of body fossils and 14 ichnogenera and, thus, represents the most diverse marine bottom fauna known so far from the Early Triassic. Our results suggest that oceanographic conditions during the early Spathian enabled ecosystems to rediversify without major abiotic limitations. However, taxonomical differentiation between habitats was still low, indicating a time lag between increasing within-habitat diversity (alpha diversity) and the onset of taxonomical differentiation between habitats (beta diversity). We suggest that taxonomical habitat differentiation after mass extinction events starts only when within-habitat competition exceeds a certain threshold, which was not yet reached in the Spathian of the investigated area. This interpretation is an alternative to previous suggestions that the prevalence of generalistic taxa in the aftermath of mass extinction events reflects protracted environmental stress. The onset of increasing beta diversity is a potential criterion for distinguishing two major recovery phases, the first ending with habitat saturation and the second ending with the completion of ecosystem differentiation.

Key words: Biotic recovery, mass extinction, palaeoecology, diversity, Early Triassic, Spathian, Virgin Formation, USA.

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Introduction

The end-Permian mass extinction is widely accepted as representing the most devastating biotic crisis in the history of metazoan life (Erwin 1993). Besides the study of the causes and mechanism of the extinction itself, the ensuing recovery interval has attracted considerable attention since the early 1990s. The paramount questions addressed in post-extinction research are, in particular, how biota and ecosystems respond to large environmental perturbations, how rapidly ecosystems can recover and how evolutionary processes proceed in vacated ecospaces.

An important but largely neglected tool in reconstructing recovery processes is that of quantitative palaeoecological studies. Although the Virgin Formation (or Virgin Limestone Member in most other studies) and related strata of the western USA have been studied in various aspects (e.g., Poborski 1954; Schubert and Bottjer 1995; Boyer et al. 2004; Pruss and Bottjer 2004; Pruss et al. 2007; McGowan et al. 2009; Pruss and Payne 2009; Mata and Bottjer 2011), very little palaeoecological community data were presented. The hitherto most comprehensive study of the Virgin palaeoecology is that of Schubert and Bottjer (1995), which, however, focused on broad patterns throughout the entire Early Triassic of the west-

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ern USA and was based on genus identification only. Although their Spathian samples exhibit the highest generic diversity and most advanced trophic structure among all Early Triassic faunas analysed, Schubert and Bottjer (1995) still concluded that the entire Early Triassic of the western USA was dominated by depauperate benthic communities reflecting a considerably delayed recovery. Schubert and Bottjer (1995: 28) suggested that this pattern largely results from the extraordinary magnitude of the end-Permian mass extinction and from intrinsic, ecological effects. Another mechanism that has been invoked to explain the putatively protracted Early Triassic recovery is that adverse environmental conditions persisted well beyond the actual extinction interval and inhibited re-diversification in the marine realm (Hallam 1991). This model was subsequently advocated by many investigators studying Lower Triassic sections from the USA (e.g., Wignall and Hallam 1992; Boyer et al. 2004; Pruss and Bottjer 2004; Mata and Bottjer 2011) as well as other palaeogeographic regions (e.g., Twitchett and Wignall 1996). However, recent studies have challenged several key aspects of this model, such as the universality of small body sizes in the Early Triassic (Brayard et al. 2010, 2011a), the existence of global shallow marine anoxia (Heydari et al. 2008), and a delayed recovery in general (Brayard et al. 2009, 2011b; Hautmann et al. 2011, Hofmann et al. 2011).

The Virgin Formation has been repeatedly studied for more or less representative palaeoecological proxies such as trace fossils (Pruss and Bottjer 2004; Mata and Bottjer 2011), shell bed architecture (Boyer et al. 2004), and microbially induced sedimentary structures (Pruss et al. 2005). All of these studies conclude that strata from this time interval in the western USA record unusual and harsh environmental conditions, such as alkaline and anoxic waters permanently (Boyer et al. 2004) or repeatedly (e.g., Pruss and Bottjer 2004) affecting shallow marine habitats and, thereby, inhibiting ecosystems from taxonomical and ecological restoration.

A study to assess the faunal heterogeneity and the recovery status of the Virgin fauna was recently provided by McGowan et al. (2009). Their data suggest that Virgin communities actually lack typical traits of post-extinction faunas such as pronounced small shell size, faunal homogeneity, low diversity and high abundances of single taxa but are comparable to faunas of the central European Muschelkalk, which were not subjected to any form of abiotic stress related to the mass extinction. Furthermore, this survey was the first to provide quantitative data on the species level and it reported an unexpectedly high bulk diversity of benthic taxa (37 species and 30 genera), including bivalves, gastropods, brachiopods, and echinoderms, which considerably exceeds the 18 genera of benthic organisms reported by Schubert and Bottjer (1995) from their Virgin localities. Hautmann et al. (2012) restudied the material of McGowan et al. (2009) and identified as many as 28 bivalve species belonging to 18 genera.

This paper presents a palaeoecological analysis of the Virgin fauna from south-western Utah based on quantitative species distribution, which is discussed in the context of depositional environments. This integrated approach helps to distil unequivocal recovery signals from "noise-variation" merely reflecting the environmental heterogeneity of shallow-marine environments and local environmental stress unrelated to actual recovery trajectories. Additionally, it allows the identification of the degree of faunal heterogeneity between adjacent habitats along environmental gradients and, thereby, the assessing of the role of beta diversity in the post-extinction diversity increase.

Institutional abbreviations.—PIMUZ, Paläontologisches Institut und Museum collection, University of Zürich, Switzerland.

Material and methods

Fieldwork was conducted by in October 2009 (by RH) and August 2010 (RH and MW) in the area of St. George and Hurricane in south-western Utah, USA. Bed-by-bed logging and documentation was undertaken at three sections in the Beaver Dam Mountains area west of St. George and at five sections along the "Honeymoon Trail", east of Hurricane (Fig. 1). This main body of data was complemented by additional observations from some single outcrops in the research area. At the studied sections, fossiliferous beds were chosen for quantitative sampling of macrofossils. The greater part of fossil material was identified and counted in the field but reference samples were taken for lab preparation and further taxonomic identification. Benthic fossils from Lower Triassic successions are notorious for their poor preservation (Schubert and Bottjer 1995; Fraiser and Bottjer 2005, Hautmann and Nützel 2005) with mostly internal and re-crystallised moulds being preserved. However, the material investigated herein is excellently preserved by Early Triassic standards and poses few problems with its taxonomic identification. Crucial taxonomic criteria are readily observable on well preserved, primarily calcitic shells of epifaunal bivalves. Internal moulds of mostly aragonitic infaunal bivalves are morphologically distinct and show no evidence of notable deformation.

The applied sampling procedure varied with respect to the sedimentary rock type and available outcrop area. Surface collections were performed mostly on shale intervals. All other samples, extracted from discrete limestone beds, were representatively sampled and mechanically decomposed for fossil collection. Each collection was performed either until it yielded more than 100 specimens or until further sampling revealed no new finds of taxa. In some cases, sampling was limited by unsuitable outcrop conditions. Beds showing evidence of strong reworking, such as pronounced gradation and size sorting, were not included in the analysis. Trace fossils were documented in the field and integrated in ecological interpretations. Identification of the sedimentological facies is based on field observations. The taxa counted include bivalves, gastropods, ammonoids, brachiopods, and sponges. The abundance of echinoderms was roughly estimated but not quanti-

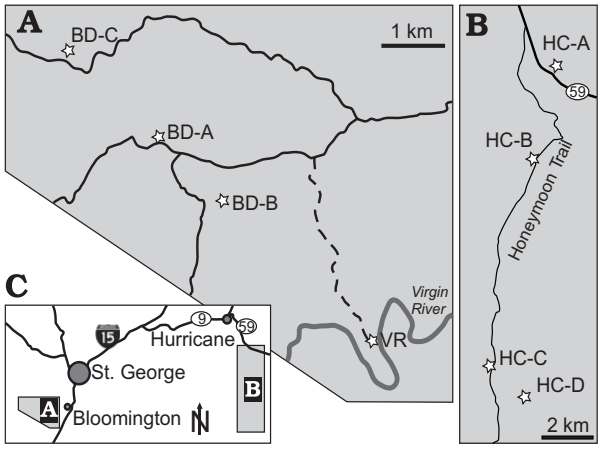

Fig. 1. Localities of the sections mentioned in the text. **A**. Beaver Dam Area. **B**. Hurricane Cliff Area. **C**. Overview map depicting the position of the study areas (**A** and **B**) around St. George, south-western Utah.

fied and their occurrences, as well as counts of trace fossils, were not considered in the cluster analyses. Most of the echinoderms were recorded by isolated plates and ossicles, which makes it impossible to estimate numbers of specimens in a given sample. Trace fossil counts are problematic, because they do not correspond with the actual abundances of their trace makers in a palaeocommunity.

Identification of bivalve taxa follows Hautmann et al. (2012).

Faunal abundance data were analysed with the software package PAST (Hammer et al. 2001). Cluster analysis was performed in order to generate groupings of samples and species on the basis of their occurrences and abundances. Most comprehensible clusters were obtained using the paired group method implanted in PAST (UPGMA, unweighted paired group with arithmetic mean) together with the Morisita index of similarity (Morisita 1959). The UPGMA algorithm (Sokal and Michener 1958) is generally recommended for taxa-in-sample data sets (Hammer and Harper 2006). The Morisita index is found to be useful in ecological studies of Recent environments (e.g., Wolda 1981) but is recommended for palaeoecolocigal data as well (Hammer and Harper 2006). The advantage of the Morisita index is that it is relatively insensitive to different sample sizes and tends to smoothen high abundances of single taxa. Samples that constitute the most resolved clusters were merged to represent one association. A comparative analysis using the Bray-Curtis similarity index (Bray and Curtis 1957), which is more sensitive to high abundances (Hammer and Harper 2006), yield essentially the same clusters, the only difference being that two samples of two adjacent associations are interchanged. Boostrapping (n = 1000) was used in order to provide a measure for robustness of clustering. Bootstrap values indicate the percentage of re-sampled replicates (random modifications of the original abundance matrix) that confirm the nodes of the computed dendrogram.

Adopted from extant ecosystem research, diversity indices are widely used in palaeobiological studies (Bambach 1977; Sepkoski 1988). Alpha (within-habitat) diversity represents the number of species in one assemblage or association which is assumed to represent the relic of a community (sensu Whittaker 1972). Beta (between-habitat) diversity expresses the taxonomic differentiation between communities or along environmental gradients (Whittaker 1972). Dominance index is defined as $D = \sum\left(\frac{n_i}{n}\right)^2$, where n is the number of individuals of taxon i (as used in PAST; Hammer et al. 2001). D is high when very few taxa or a single taxon dominates a community, and D is low when many taxa are present in similar abundances. The trophic nucleus of an association is defined by those taxa that contribute to 80% of the total specimen number per association (Neyman 1967).

Geological background

Notes on the stratigraphic nomenclature.—The stratigraphic nomenclature of Spathian deposits of the western USA, usually referred to as Virgin Limestone Member (e.g., Schubert and Bottjer 1995; Pruss and Bottjer 2004; Mata and Bottjer 2011), remains somewhat unclear. Poborski (1954) recommended abandoning the somewhat misleading term "limestone" (the Virgin is mainly composed of siltstone). Furthermore, the "Virgin Limestone" has been raised into formational rank and, consequently, the Moenkopi Formation into group status (Poborski 1954). Recently, this concept found agreement from Lucas et al. (2007) and Godspeed and Lucas (2007). Additionally, Lucas et al. (2007) emended the stratigraphic scheme of Lower Triassic Rocks in the western USA by assigning all marine strata to the Thaynes Group and all non-marine deposits to the Moenkopi Group. Although this procedure appears reasonable, problems may arise because the distinction between marine and non-marine facies can be equivocal. Unquestionably, Virgin-type strata represent mostly shallow and marginal marine wedges that are equivalent to the fully marine Thaynes Group, but in the investigated area, no typical Thaynes lithology is developed, and Virgin-type strata are exclusively found in south-western Utah and eastern Nevada. Therefore, we follow Poborski (1954) in treating Virgin-type deposits of south-western Utah as the Virgin Formation of the Moenkopi-Group (Fig. 2). This view seems to be the most applicable solution according to articles 24 and 25 of the North American Stratigraphic Code (NACSN 2005).

Geological setting and stratigraphy.—During the Early Triassic, much of the western USA was part of an epicontinental marine basin connected to the Panthalassic Ocean to the west (Fig. 3). The depot centre was presumably situated in an area stretching from the northwestern part of Utah towards central and western Nevada (Blakey 2011). In the course of several transgressions and regressions, shore-

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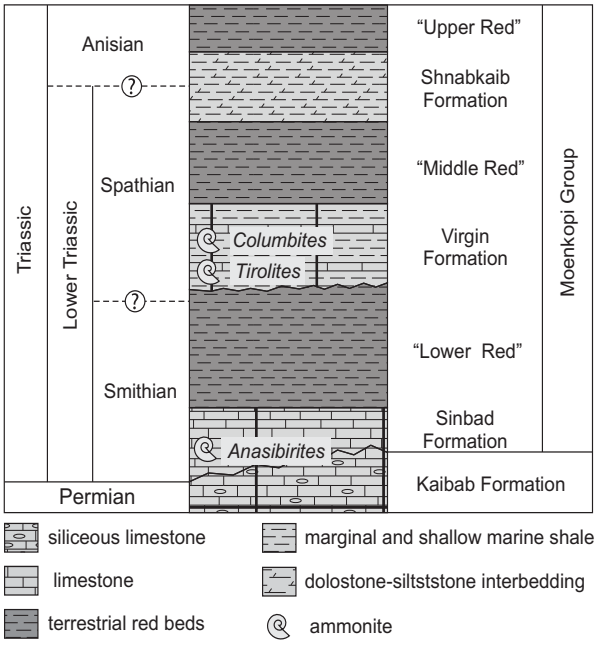

Fig. 2. Lithostratigraphic column of the Moenkopi Group in the investigated area. Thickness of lithostratigraphic units and the position of ammonite markers are schematic and not to scale. Presence of *Anasibirites* after Lucas et al. (2007), *Tirolites* after Poborski (1954), and *Columbites* after Bucher in Hautmann et al. (2012).

lines shifted considerably over the area, but the approximate maximum extent of marine strata during the Early Triassic is documented in south-western and south-central Utah, with marine tongues transgressing over terrestrial and marginal marine red beds during Smithian (Sinbad or Timpoweap Formation) and Spathian (Virgin Formation) times. The lower contact of the Virgin Formation to the underlying "Lower Red" is marked by an unconformity, which represents either a gap in sedimentation accompanied by erosion, or truncation during shoreline retreat. The heterogeneity of the earliest Virgin-type deposits within short distances, however, suggests that the initial Virgin transgression drowned a considerable land relief. The transition to the overlying "Middle Red" has not been observed. At all the localities studied, the contact between the Virgin Formation and the "Middle Red" was concealed, or the Virgin Formation represented the top of local sections. In the type area, the Virgin Formation is mainly composed of calcerous siltstone, claystone, calcarenite and bioclastic grainstone. These lithotypes generally represent deposits of shallow subtidal and intertidal environments including open and protected marine systems of a tropical to subtropical setting, under arid climate (Reif and Slatt 1979).

Based on lithostratigraphic considerations, the Virgin Formation has been generally assumed to be Spathian in age (Reeside and Bassler 1922). Poborski (1954) mentioned the presence of the ammonite *Tirolites spinosus* in the middle part of the formation. Unfortunately, no figures were presented, but other workers (e.g., Bissell 1973) confirmed this identification. *Tirolites* is a common ammonite genus of lowermost Spathian strata worldwide and a characteristic element of the first two Spathian ammonite zones (e.g., Galfetti et al. 2007; Guex et al. 2010). Recent fossil collections (McGowan et al. 2009) yielded an ammonoid specimen from middle part of the Formation, which has been identified as *Columbites parisianus* (Bucher in Hautmann et al. 2012), suggesting a late Early Spathian age (Guex et al. 2010). The *Tirolites*/*Columbites*-beds from China were calibrated with zircon U-Pb data, which indicate an age of 250.6±0.5 Ma for this ammonite zone (Ovtcharova et al. 2006), approximately 2 Ma after the main extinction (Mundil et al. 2004).

Sedimentary environments of the Virgin Formation

Beaver Dam Mountains (sections BD-A, BD-B, and VR) (Fig. 4).—In this area, the Virgin Formation attains a thickness of 34 m and is mainly composed of calcareous siltstone and shale, interbedded with distinct ledge-forming limestone beds. As exposed in the sections BD-A (Fig. 4A) and BD-B (Fig. 4B), the base of the Virgin is composed of ca. 2 m thick, mainly through cross-bedded and occasionally planar-bedded,

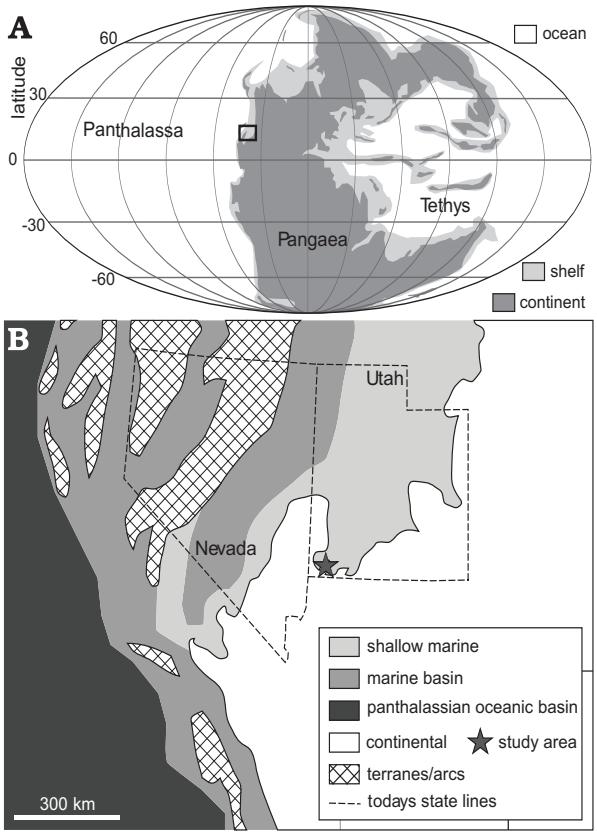

Fig. 3. Palaeogeographic restorations after Blakey (2011). **A**. Global palaeogeography of the Early Triassic. **B**. Early Triassic palaeogeography of the western USA.

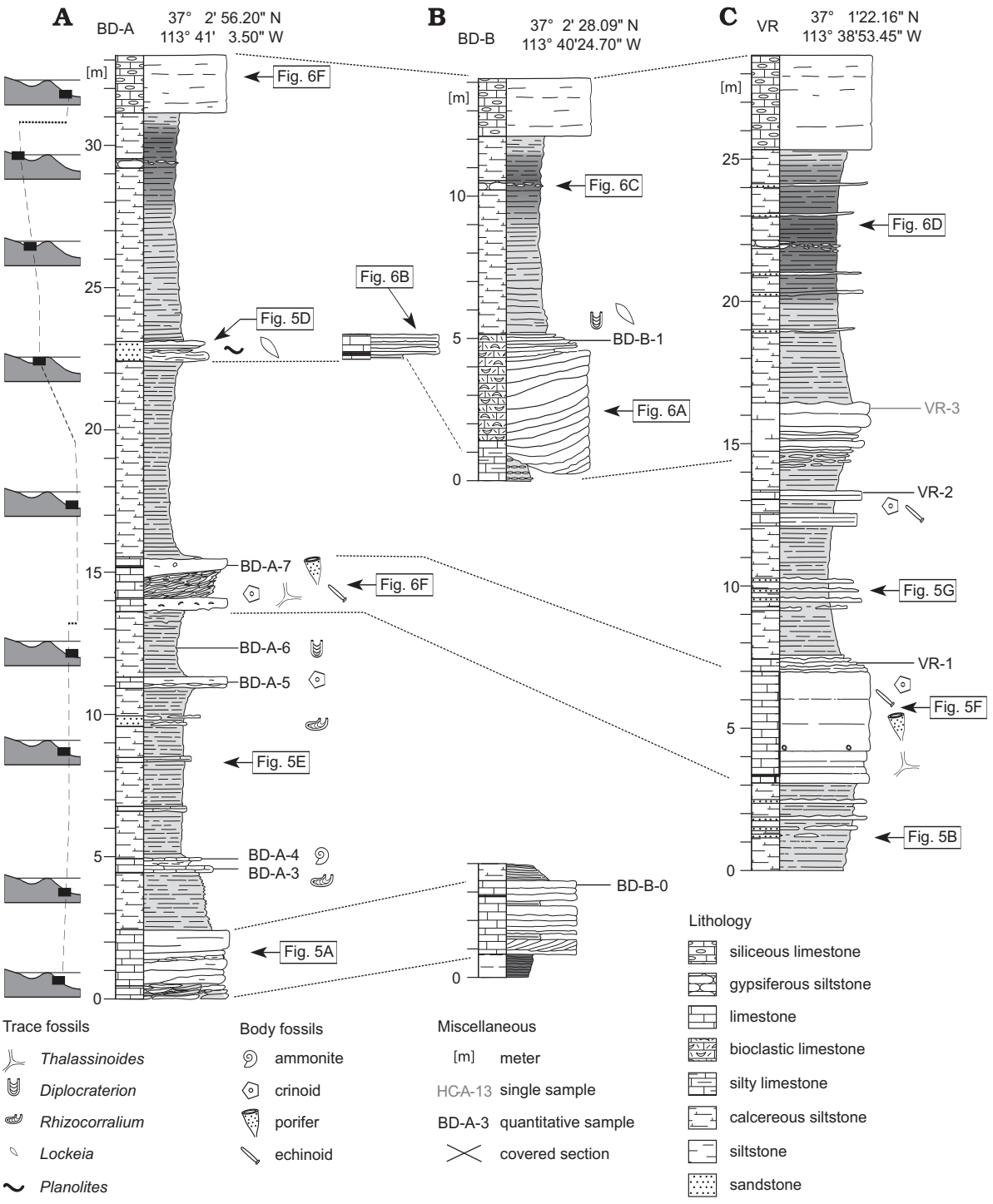

Fig. 4. Stratigraphic sections shown as weathering profile of the Spathian, Lower Triassic in the Beaver Dam Mountains area, Utah, USA. Bathymetric interpretation on the left. Locality map see Fig. 1B. **A**. Section BD-A. **B**. Section BD-B. **C**. Section VR.

sandy packstone and grainstone (Fig. 5A). These beds are interpreted as shallow subtidal bars of the shoreface zone. These are succeeded by 12 m of maroon siltstone interbedded with thin limestone layers (BD-A) or massive and ripple cross-laminated, very fine-grained sandstone (VR; Fig. 5B). This points to alternating suspension fall out under quiet water conditions

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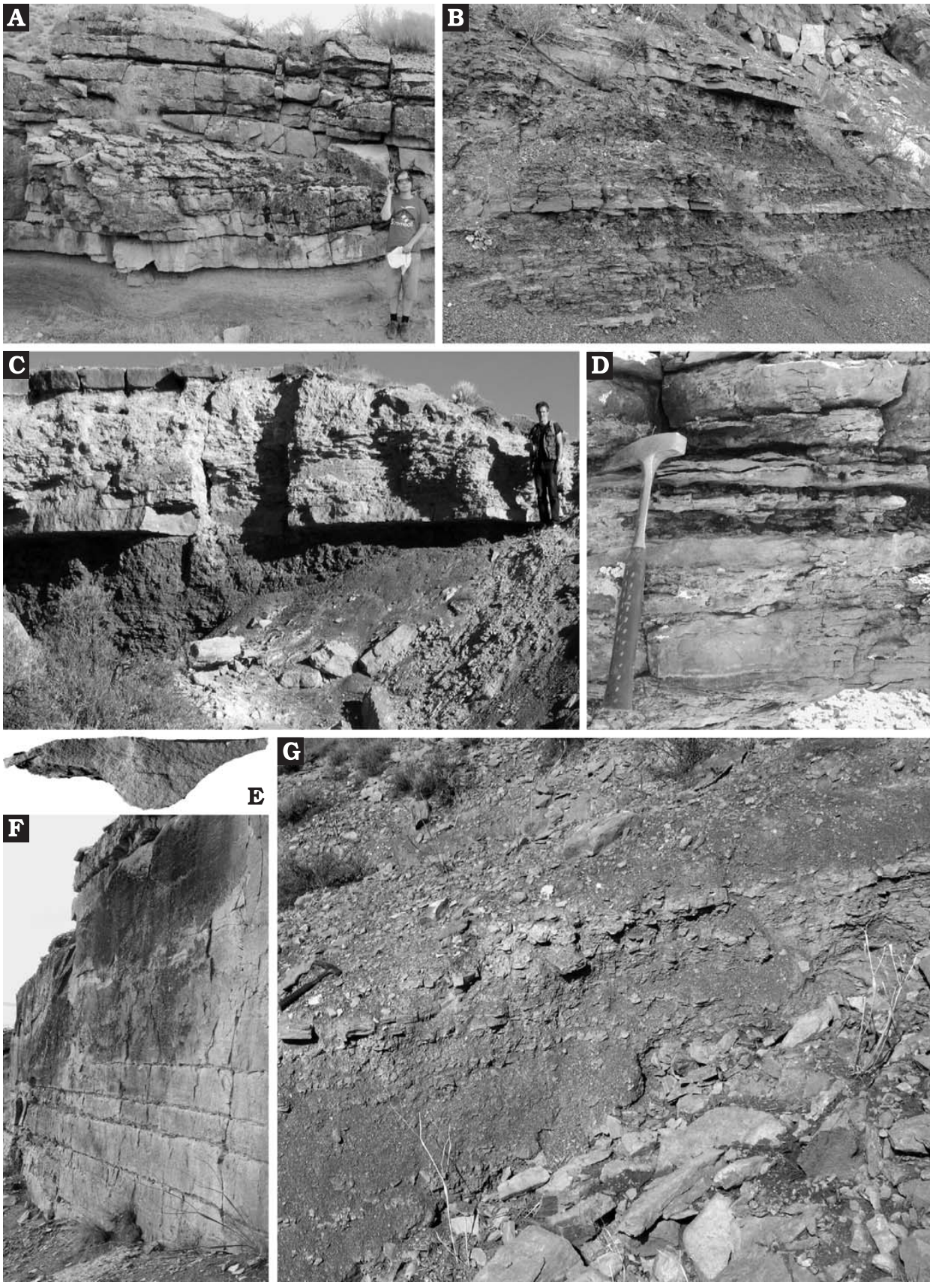
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and the activity of waves and currents. Accordingly, this interval is interpreted as deposits of the lowermost shoreface to offshore transition zone. Short transgressive events lead to the rhythmic deposition of discrete limestone beds. Evidence for erosional events possibly caused by minor storms is provided by the presence of small guttercasts (Fig. 5E) within the siliclastic intervals (Myrow 1992).

A second prominent unit of massive, silty and sandy limestone is observed in the middle part of the section BD-A (Fig. 5C) and within the lower half of section VR (Fig. 5F). These limestone beds record a transgressive event leading to a decline in siliciclastic input. The presence of sponges in these beds suggests low detrital input, too. The amalgamated character of these massive limestone beds and the concentration of comparably large sponge fragments at the base of this interval suggest that these beds were deposited under storm influence in the lower shoreface zone. The beds are overlain by bluish-grey, highly calcareous siltstone interbedded with thin limestone beds (Fig. 5G). This siltstone interval is ca. 7 m thick and represents deposits of lower shoreface and offshore transition zone, similar to the lower siltstone beds with few limestone and rippled sandstone beds.

In the section BD-A and VR, this interval is overlain by a 1 to 1.5 m thick sequence of ripple cross-laminated, slightly calcareous sandstone showing flaser bedding and mud drapes (Fig. 5D). These sandstone beds most likely record tidal flat deposits of the lower intertidal zone. The same stratigraphic level in the BD-B section is represented by an up to 5 m thick succession of large scale through cross-bedded, bioclastic grainstone (Fig. 6A). These beds are incised into the underlying siltstones and show a channel-like morphology pinching out towards NW and SE, giving rise, laterally and horizontally to thin beds of parallel cross and planar bedded, bioclastic grainstone (Fig. 6B). These lithotypes are interpreted as tidal inlets deposits representing lateral equivalents of the tidal flat recorded in section BD-A and VR.

In all sections of the Beaver Dam Mountains area, the succeeding interval is composed of purple to reddish siltstone, occasionally interbedded with thin sandstone beds (Fig. 6D). In the upper third of this interval, gypsiferous levels are observed within red, massive to finely laminated siltstone (Fig. 6C). This succession is interpreted as upper intertidal mudflat deposits grading into a supratidal plain with possible early pedogenetic caliche horizons (Fig. 6D). This level is overlain by ca 0.5 m of yellow and bluish-grey, highly calcareous siltstone, once again, recording marine conditions (Fig. 6D). The top of the Virgin Formation is capped by massive, slightly siliceous, recrystallised limestone with a thickness of 2–3 m (Fig. 6F). This unit is difficult to interpret because of the absence of macrofossils and indicative sedimentary structures.

Hurricane Cliff (sections HC-A, HC-B, HC-C, HC-D) (Fig. 7).—In the sections cropping out east of the Hurricane Cliff, the Virgin Formation is up to 20 m thick, but as in the case of section HC-C, the base varies considerably, which leads locally to increased cumulative thicknesses. The lithological succession is variable and in particular the lowermost carbonate-dominated unit is different in some sections. These sections are treated separately in the following paragraphs.

HC-A (Fig. 7A).—Here, the base is developed as a 5 m thick succession of sandy limestone (Fig. 6G). The lower part is dominated by up to 1 m thick sets of cross-bedded grainstone alternating with thin planar-bedded, silty grainstone beds, which are highly bioturbated. Herring bone cross-stratification (Fig. 6G) and occasionally mud-drapes and sigmoidal cross bedding are frequently observed. All of these sedimentary structures suggest a strong tidal influence with alternating high energy flow regime and slack water periods and alternating current directions (Kreisa and Moiola 1986). These limestone beds alternate with thin, highly bioturbated horizons (Fig. 6E). The upper part of this lower limestone is dominated by thinly bedded, slightly heterolithic, silty limestone. The top is capped by trough cross-bedded grainstone (Fig. 6H). This complex is interpreted as tidal channel deposits or small scale tidal inlets of the lowermost intertidal to shallow subtidal zone.

These beds are overlain by a succession of bluish-grey, calcareous siltstone and fine-grained sandstone which most likely record the deposition around the upper offshore transition and the lower shoreface. This interval is followed by 50 cm of alternating laminated siltstone and ripple cross-laminated, fine-grained sandstone showing flaser bedding and slight bioturbation (lowest bed in Fig. 8A). The following 1.5 meters are composed of maroon, very finely-laminated, slightly heterolithic siltstone beds (Fig. 8A). This whole siliclastic dominated interval most likely represents a shallowing-upward succession ranging from lower shoreface zone to an intertidal succession that includes sand-dominated mixed flat depostis of lower intertidal zone and deposits of upper intertidal mudflats (Klein 1971).

At 8.5 m, 2 meters of bluish grey siltstones, similar to those in the lower part of this fine-grained interval occur. The base of this siltstone is slightly irregular (Fig. 8A). A 30 cm thick bed of massive and ripple cross-laminated sandstone and siltstone is intercalated within this siltstone interval. This siltstone-dominated part of the section is capped by ca. 1 m thick, trough cross-bedded sandy packstone (Fig. 8E). The

← Fig. 5. Sedimentary facies of the Spathian, Lower Triassic in the Beaver Dam Mountains area, Utah, USA. **A**. Subtidal bars composed of trough cross-bedded grainstone at the base of the Virgin Formation at section BD-A. **B**. Claystone interbedded with thin beds of fine-grained sandstone deposited in the offshore transition. Base of section VR. The height of the exposure is 1.80 m. **C**. Ledge of sandy and silty limestone deposited in the lower shoreface. Lower part of section BD-A. **D**. Fine-grained sandstone showing flaser bedding of the sand flat facies. Upper part of Section BD-A. Hammer for scale. **E**. Cross sectional view of a gutter cast from the lower siltstone interval of section BD-A. **F**. Massive, amalgamated grain, and packstone of the lower shoreface. Lateral equivalent to the bed shown in Fig. 5C. Section VR. Height of exposure is 4 m. **G**. Interbeddings of calcareous siltstones and thin limestone. Section VR. The hammer is 35 cm long.

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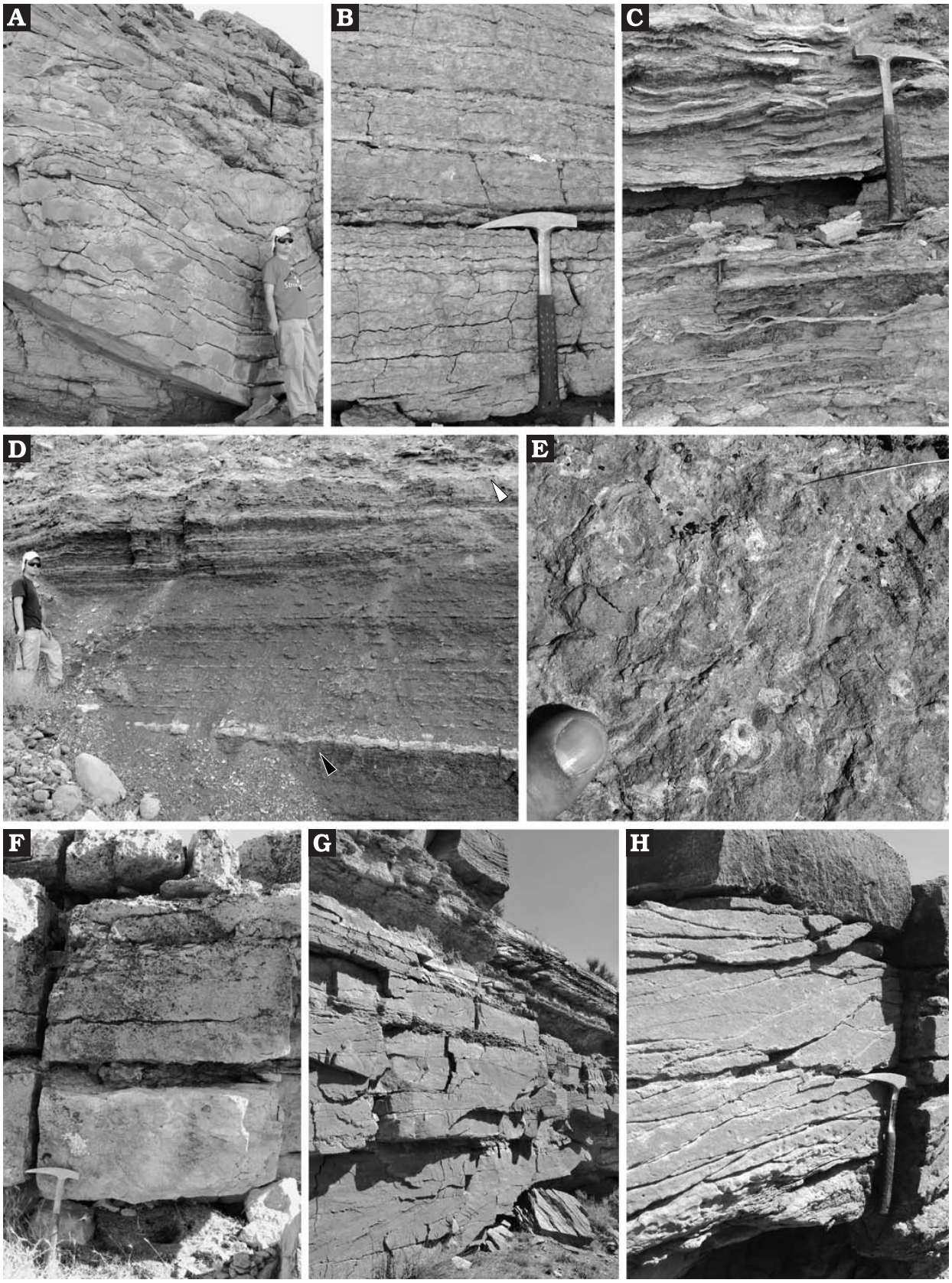
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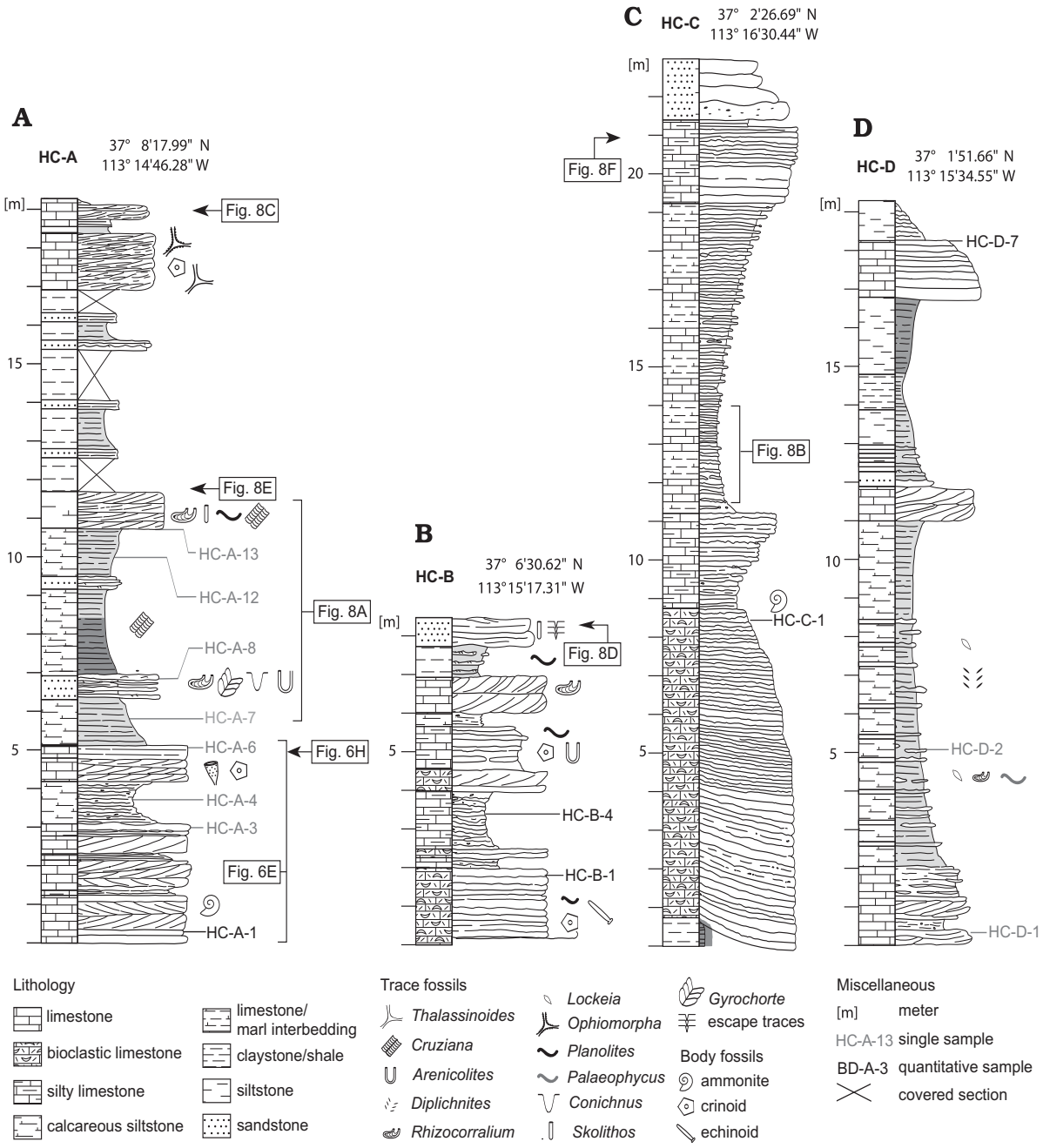

Fig. 7. Stratigraphic sections shown as weathering profile of the Spathian, Lower Triassic in the Hurricane Cliffs area, Utah, USA. See Fig. 1B for locality map. **A**. Section HC-A. **B**. Section HC-B. **C**. Section H-C. **D**. Section HC-D.

← Fig. 6. Sedimentary facies of the Spathian, Lower Triassic in the Beaver Dam Mountains and the Hurricane Cliffs area, Utah, USA. **A**. Large scale trough cross-bedded grainstone of the tidal inlet facies at section BD-B. **B**. Lateral equivalent of the same bed as in A showing parallel bedding of skeletal grainstone. Hammer for scale. **C**. Gypsiferous siltstone of the supratidal and continental red bed facies in the upper part of section BD-B. **D**. The same interval as shown in C at the section VR. The black arrow head points to a discrete horizon characterised by nodular gypsum. In the upper part (white arrow head), marine calcareous siltstones mark a short trangression at the close of the marine Virgin deposition. **E**. Highly bioturbated bedding plane dominated by *Palaeophycus* observed in the basal limestone unit of Section HC-A. **F**. Siliceous limestone capping the section BD-A. Hammer for scale. **G**. Basal limestone unit of the section HC-A showing abundant and various types of cross bedding. Height of exposure is 5 m. **H**. Top of the basal limestone unit at section HC-A showing trough cross-stratified grainstone beds. The hammer is 35 cm long.

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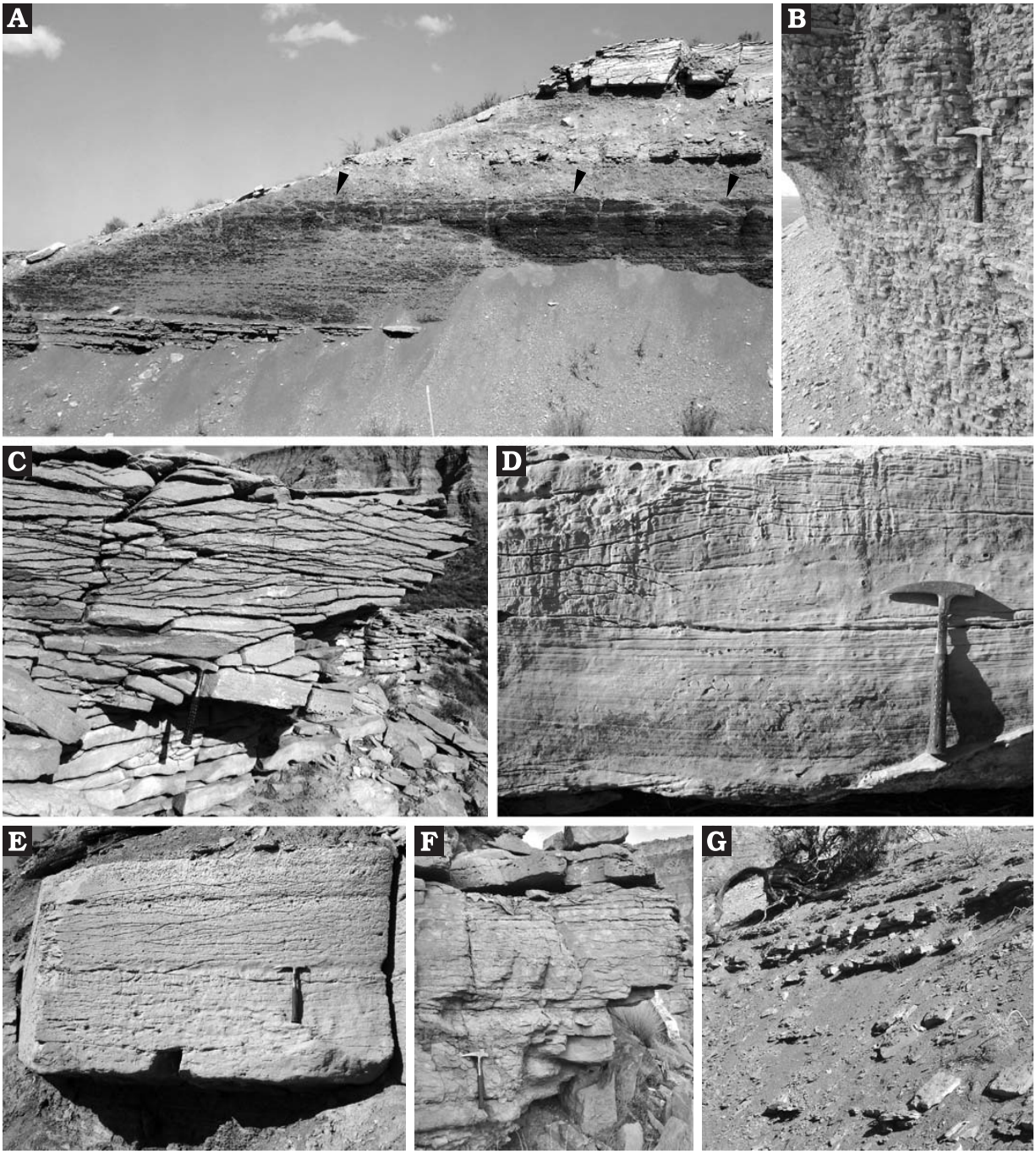

Fig. 8. Sedimentary facies of the Spathian, Lower Triassic in the Hurricane Cliffs area, Utah, USA. **A**. Middle part (~ 6–12 m) of the Virgin Formation at section HC-A showing the transition between lagoonal and intertidal siltstone to the overlying open marine siltstone. The black arrow heads point to the transgressive surface. Height of exposure is 6 m. **B**. Alternating marls and limestone in the middle part of the section HC-C interpreted as channel fill of the tidal inlet complex. **C**. Trough cross-bedded, highly sandy limestone of the upper shoreface capping the section HC-A. **D**. Hummocky cross-bedded sandstone with *Skolithos* isp. forming the top of section HC-B. **E**. Sandy limestone of the shoreface in the middle part (11 m) of section HC-A. **F**. Parallel stratified grainstone beds forming the topmost beds of HC-C. **G**. Lagoonal siltstone of the lower part of section HC-D. Height of exposure is 3 m. The hammer is 35 cm long.

remaining part of the section is composed of alternating grey siltstone intercalated with some thin fine-grained sandstone. The top is composed of trough cross-bedded sandy limestone (Fig. 8C). The fine-grained intervals in this upper part are largely covered, which makes facies identification difficult. Mata and Bottjer (2011) interpreted this portion as deposits of the offshore transition zone. However, the top of the section HC-D, which is likely to represent a lateral equivalent, is

Table 1. Body fossils found in the Spathian, Lower Triassic Virgin Formation during this study and their ecological classification. Mode of life: n, nektonic; mi,mobile infaunal; ssi, stationary semi infaunal; se, stationary epifaunal; me, mobile epifaunal. Trophic groups: sf, suspension feeder; df, deposit feeder; c, carnivore; g, grazer; psc, primary or secondary consumer. Echinodermata and ichnia were not included in the cluster analysis.

	Species	Trophic guild
Bivalvia	Astartidae spp.	mi, sf
	Bakevellia costata (Schlotheim, 1820)	ssi sf
	Bakevellia exporrecta (Lepsius, 1878)	ssi sf
	Eumorphotis cf. *venetiana* (Hauer, 1850)	se sf
	Eumorphotis cf. *multiformis* (Bittner, 1899)	se sf
	Eumorphotis ericius Hautmann, Smith, McGowan, and Bucher, 2013	se sf
	Eumorphotis virginensis Hautmann, Smith, McGowan, and Bucher, 2013	se sf
	Leptochondria curtocardinalis (Hall and Whitfield, 1877)	se sf
	Leptochondria nuetzeli Hautmann, Smith, McGowan, and Bucher, 2013	se sf
	Myalinella sp. A	me, sf
	Neoschizodus laevigatus (Zieten, 1830)	mi, sf
	Pernopecten sp. A	me, sf
	Promyalina putiatinensis (Kiparisova, 1938)	se sf
	Promyalina spathi (Newell and Kummel, 1942)	se sf
	Protopis sp.	se sf
	Sementiconcha recuperator Hautmann, Smith, McGowan, and Bucher, 2013	mi, sf
	Trigonodus cf. *sandbergeri* Alberti, 1864	mi, sf
	Trigonodus cf. *orientalis* Alberti, 1864	mi, sf
	Unionites cf. *canalensis* (Catullo, 1846)	mi, sf
	Unionites cf. *fassaensis* (Wissmann in Münster, 1841)	mi, sf
Gastropoda	*Natiria* cf. *costata* Münster, 1841	me, g
	Gastropod ind. A	me, g
Ammonoida	*Tirolites* sp. A	n, psc
	Ammonite ind. A	n, psc
	Ammonite ind. B	n, psc
Brachiopoda	*Piarorhynchella triassica* (Girty in Mansfield, 1927)	se, sf
	Protogusarella smithi Perry and Chatterton, 1979	se, sf
Porifera	*Cypellospongia* sp. A	se, sf
Echinodermata	*Holocrinus smithi* (Clark in Clark and Twitchell, 1915)	se, sf
	Miocidaris utahensis (Kier, 1968)	me, g
Ichnia	*Conichnus* isp.	se, sf
	Cruziana problematica (Schindewolf, 1928)	me, df/c
	Diplichnites isp.	me, df/c
	Diplocraterion isp.	mi, sf
	Gyrochorte cf. *comosa* Heer, 1865	mi, df
	Lockeia siliquaria James, 1879	mi, sf
	Ophiomorpha isp.	mi, df
	Palaeophycus tubularis Hall, 1847	mi, sf/c
	Planolites montanus Richter, 1837	mi, df
	Rhizocorallium isp	mi, sf
	Spongeliomorpha isp.	mi, df
	Skolithos isp.	mi, sf
	Thalassinoides cf. *suevicus* (Rieth, 1932)	mi, df
	Arthropod trackway	mi,df/c

herein suggested as representing lagoonal deposits (see section HC-D). The following grainstone beds, which are mainly composed of crinoidal debris, are similarly difficult to interpret because trough cross bedded crinoidal limestone occur in various settings ranging from shallow to deep marine as discussed in Mata and Bottjer (2011). However, the finding of a comparatively large articulated columnal segment of *Holocrinus smithi* (Fig. 9E) suggests that these beds record conditions very close to the living site of the crinoids, which were bound to shallow water conditions during Palaeozoic and Mesozoic times. We therefore suggest that the upper part of the section HC-A represents shallow sub-

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Table 2. Data matrix showing absolute abundances of species in the samples. Occurences of *Holocrinus smithi* and *Miocidaris utahensis* are estimated and were not included in the cluster analysis. Abbreviations: a, abundant; c, common; r, rare; vr, very rare.

Species	Samples													
	BD-A-4	BD-A-6	HC-A-1	VR-1	BD-A-7	BD-A-5	BD-B-1	BD-B-0	VR-2	BD-A-3	HC-B-1	HC-C-1	HC-B-4	HC-D-7
Astartidae sp. A	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Bakevellia costata	0	0	1	1	8	1	0	7	0	8	0	0	5	37
Bakevellia exporrecta	103	25	12	7	0	0	7	19	0	34	0	2	0	0
Eumorphotis cf. *venetiana*	1	0	0	0	4	1	0	11	0	0	0	0	6	0
Eumorphotis cf. *multiformis*	5	0	0	6	5	0	0	3	3	0	0	3	0	1
Eumorphotis ericius	3	0	0	12	36	9	21	9	35	31	0	1	0	0
Eumorphotis virginensis	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Leptochondria curtocardinalis	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Leptochondria nuetzeli	41	40	0	5	4	0	0	0	0	14	0	0	0	0
Myalinella sp. A	0	0	0	0	6	0	0	0	0	1	0	0	0	0
Neoschizodus laevigatus	0	0	0	5	0	0	0	0	3	0	0	0	0	0
Pernopecten sp. A	0	0	0	0	5	1	0	0	1	0	0	0	0	0
Promyalina putiatinensis	3	0	11	9	10	2	40	7	39	5	0	0	1	0
Promyalina spathi	0	0	0	0	0	0	0	0	0	0	0	0	0	15
Protopis sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Sementiconcha recuperator	89	0	0	0	0	0	0	3	1	19	0	0	0	0
Trigonodus cf. *sandbergi*	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Trigonodus cf. *orientalis*	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Unionites canalensis	1	0	0	0	1	0	0	0	0	0	0	0	0	0
Unionites fassaensis	2	0	0	0	1	0	0	3	2	4	0	0	0	0
Natiria cf. *costata*	0	0	0	0	0	0	0	2	0	2	0	0	0	0
Gastropod ind. A	0	0	1	0	1	0	0	6	0	1	0	1	0	0
Piarorhynchella triassicus	4	0	0	0	4	1	100	24	31	2	20	97	0	0
Protogusarella smithi	0	0	0	0	12	0	400	50	48	59	5	2	0	0
Ammonite ind. A	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Tirolites sp. A	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Ammonite ind. B	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Cypellospongia sp. A	0	0	0	0	7	2	0	0	0	0	0	0	0	0
Holocrinus smithi	0	0	0	c	c	c	0	r	c	0	r	0	c	0
Miocidaris utahensis	0	0	0	r	a	c	r	vr	c	0	c	r	0	0

tidal bars alternating with quiet water conditions of protected marginal marine embayments.

HC-B (Fig. 7B).—This ca. 8 m thick interval largely corresponds with the lower series of limestone beds of section HC-A. The first five meters are readily comparable, although, the thicknesses of the silty limestone beds are variable in comparison to HC-A. These beds are interpreted as deposits of the shoreface zone as well. The base of the shaly interval from section HC-A is here marked by an interval of siltstones containing patches of fine-grained ripple cross-laminated sandstone capped by a 30-cm-thick bed of fine-grained hummocky cross stratified sandstone (Fig. 8D). This supports the interpretation of this interval as deposits of the lowermost shoreface and upper offshore transition (Cheel and Leckie 1993).

HC-C (Fig. 7C).—The first 9 m of this section are entirely composed of large-scale through cross-bedded bioclastic grainstone beds. Individual beds are variable in thickness, ranging from 3 cm to 20 cm and are occasionally separated by mud drapes. This interval varies laterally on outcrop scale, pinching out within less than 200 meters towards the north. These beds grade upsection into a 2.5 m thick interval of sandy, planar-bedded grainstone.

The next 8 m of this section comprise rhythmic interbeddings of 3–5 cm thick marlstone and 1–4 cm thick limestone beds (Fig. 8B). Internal sedimentary structures are not observed. This interval shows a thickening upward cycle with decreasing thickness of the marlstone beds. The unit is capped by a 2 m thick interval of planar bedded sandy limestone (Fig. 8F). The top of the section is made up of 1.5 m of slightly calcareous, fine-grained sandstone. This whole suc-

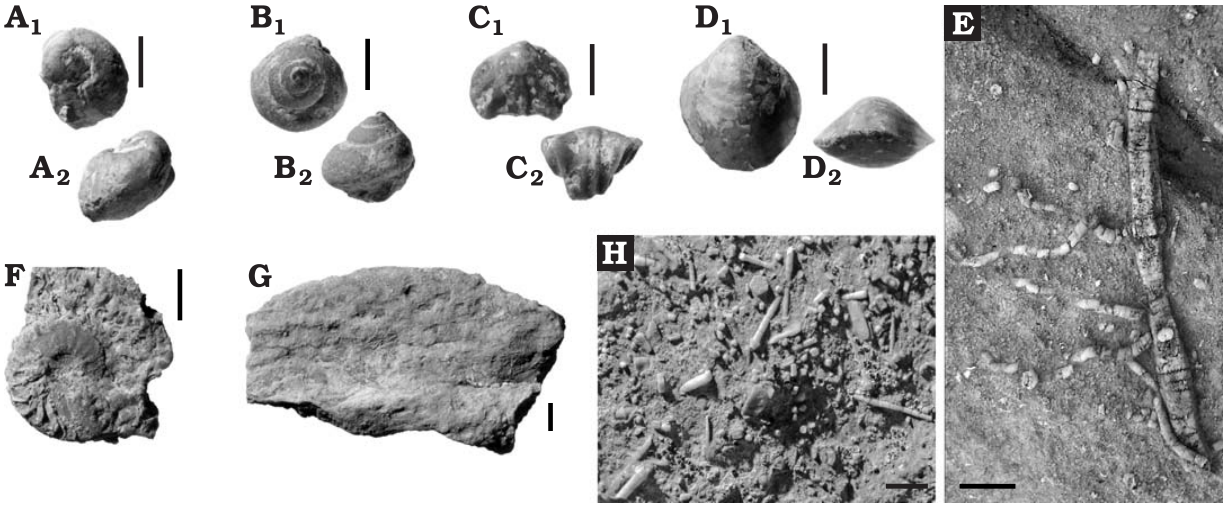

Fig. 9. Fossils of the Spathian (Lower Triassic) Virgin Formation, Utah, USA. **A**. *Natiria* cf. *costata*, PIMUZ29595. **B**. Gastropod ind. A, PIMUZ29594. **C**. *Piarorhynchella triassica*, PIMUZ29589. **D**. *Protogusarella smithi*, PIMUZ29612. **E**. Fieldphotograph of *Holocrinus smithi*. Topmost limestone of Section HC-A. **F**. *Tirolites* sp. A, PIMUZ29591. **G**. *Cypellospongia* sp. A, PIMUZ29598. **H**. Spines of *Miocidaris utahensis*, PIMUZ29611. Scale bars 5 mm.

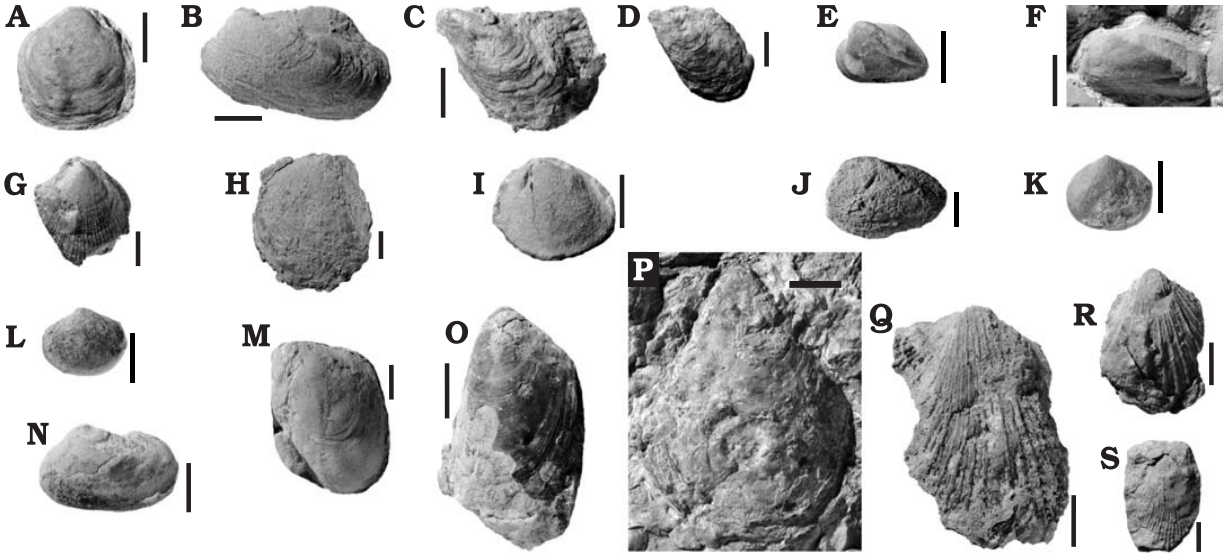

Fig. 10. Fossil bivalves from the Spathian (Lower Triassic) Virgin Formation, Utah, USA. **A**. Astartidae sp. A, PIMUZ29588. **B**. *Bakevellia exporrecta*, PIMUZ29592. **C**. *Bakevellia costata*, PIMUZ29614. **D**. *Myalinella* sp. A, PIMUZ29597. **E**. *Sementiconcha recuperator*, PIMUZ29600. **F**. *Protopis* sp. A, PIMUZ29609. **G**. *Leptochondria nuetzeli*, PIMUZ29615. **H**. *Eumorphotis virginensis*, PIMUZ29616. **I**. *Neoschizodus laevigatus*, PIMUZ29599. **J**. *Trigonodus* cf. *sandbergeri*, PIMUZ29603. **K**. *Trigonodus* cf. *orientalis*, PIMUZ29604. **L**. *Unionites* cf. *fassaensis*, PIMUZ2960. **M**. *Promyalina spathi*, PIMUZ296102. **N**. *Unionites* cf. *canalensis*, PIMUZ29596. **O**. *Promyalina putiatinensis*, PIMUZ29601. **P**. *Pernopecten* sp. A., PIMUZ29590. **Q**. *Eumorphotis ericius*, PIMUZ29587. **R**. *Eumorphotis* cf. *multiformis*, PIMUZ29613. **S**. *Eumorphotis* cf. *venetiana*, PIMUZ29593. Scale bars 5 mm; except O, P, Q 10 mm.

cession is interpreted as a large tidal inlet complex with a subsequent channel fill.

HC-D (Fig. 7D).—This 19 m thick succession is composed of an alternation of fine-grained, shale-dominated intervals with some prominent limestone ledges. The lowermost 2 m comprise trough cross-bedded, highly sandy grainstone and silty, indistinctly planar bedded packstone, and grainstone. Mud drapes are frequently observed along individual cross sets. This lower unit is interpreted as shallow subtidal to lower intertidal deposits. The following 9 m thick interval (Fig. 8G) is composed of slightly calcareous siltstone beds, which are intercalated with thin, fine-grained, combined flow ripple cross-laminated sandstone beds that yield comparably well preserved trace fossils (see chapter Biological sed-

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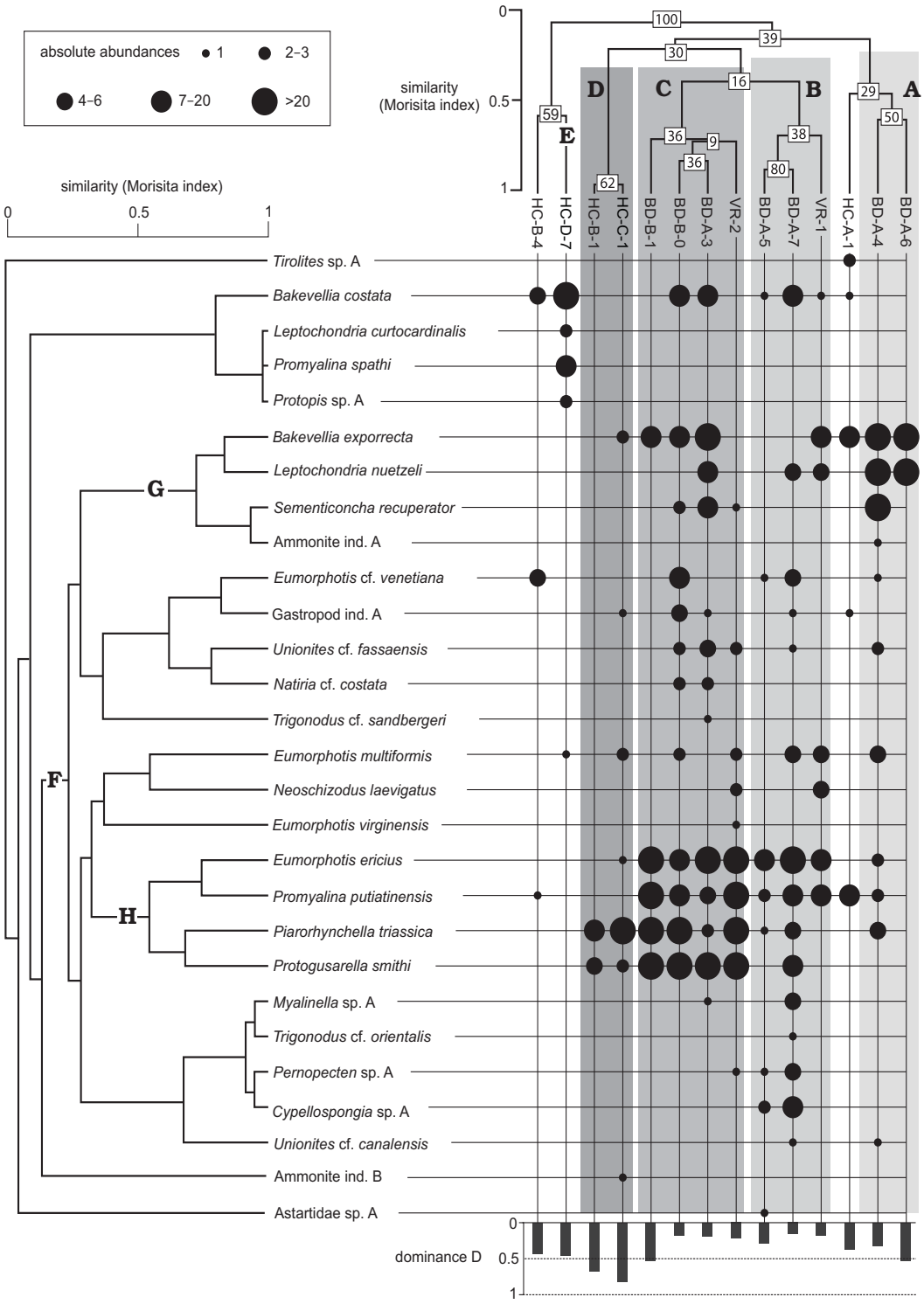

Fig. 11. Q (samples) and R-mode (species) cluster analysis using the unweighted paired group algorithm and Morisita index of similarity. Classes of abundances (circle size) represent the quintiles of absolute-abundance frequencies. Bootstrap values are shown in the white boxes within the Q-mode cluster. Dominance is given as D = 1-Simpson index. **A**. *Bakevellia exporrecta* Association. **B**. *Eumorphotis ericius* Association. **C**. *Protogusarella smithi* Association **D**. *Piarorhynchella triassica* Association. **E**. *Bakevellia costata* Assemblage. **F**. Main R-mode cluster incorporating the nuclei of several associations. **G**. Subcluster reflecting the nucleus of the *Bakevellia exporrecta* Association and it probably incorporates those species, which are adapted to low energy, softground conditions. **H**. Subcluster reflecting the nuclei of the *Eumorphotis ericius* Association and *Protogusarella smithi* Association, and it incorporates species adapted to high energy, near shore conditions.

imentary structures) and wrinkle marks. This shale interval predominantly records quiet water conditions. Some characteristics such as the lack of marine body fossils, and the presence of discrete rippled sandstone beds points to deposition within a protected embayment or lagoon. A 1 m thick bed of trough cross-bedded grainstone is developed above. The next 5 m are composed of shale similar to those described above. However, the uppermost 1.5 m are maroon in colour, and rippled sandstone is absent. The section is capped by 2 m of planar bedded sandy and silty limestone, which grade upwards into thin, indistinctly planar bedded siltstone. This upper part is interpreted as deposits of a marginal marine embayment.

Palaeoecology of the Virgin Formation

The Virgin fauna.—In terms of abundance and diversity, the main constituents of the Virgin fauna are bivalves with 20 species reported herein. Locally, numerical dominant elements are brachiopods (two species). More rarely recorded are gastropods (two species) and sponges (one species). Echinoids and crinoids are represented by one species each. Nekton is represented by rare finds of ammonites (three species), which are presented in open nomenclature due to their poor state of preservation. In general, our study confirms the taxonomic composition and overall diversity of recent analyses of the Virgin Formation (McGowan et al. 2009; Hautmann et al. 2012). The whole faunal content is shown in Table 1. All body fossils mentioned in this study are illustrated in Figs. 9 and 10.

Results of the Q-mode cluster analysis (faunal associations and assemblages).—In the Q-mode cluster analysis, samples are grouped into clusters that are similar with respect to presence and abundance of taxa. The result of the cluster analysis is shown in Fig. 11. Absolute abundance data for each sample are given in Table 2. There are four associations (recurrent assemblages) and one assemblage recognised in the data set, which in the first place reflect varying abundances rather than a different content of taxa. Owing to the homogenous composition of the Virgin fauna, groupings of samples are not very robust. Bootstrap values (Fig. 11) indicate that most branches show low reproducibilities.

***Bakevellia exporrecta* Association**.—This association (Fig. 12) is represented by the samples BD-A-4 and BD-A-6. The trophic nucleus comprises semi-infaunal (*Bakevellia exporrecta*) and epifaunal bivalves (*Leptochondria nuetzeli*). In BD-A-4, the shallow infaunal (*Sementiconcha recuperator*) is extremely abundant, and a few other, mostly epifaunal bivalves are recorded in very small numbers (e.g., *Eumorphotis ericius*, *Promyalina putiatinensis*). Species richness ranges from 2 to 11 (mean average = 6.5) and dominance D is relatively high, ranging from 0.32 to 0.53 (mean average = 0.42).

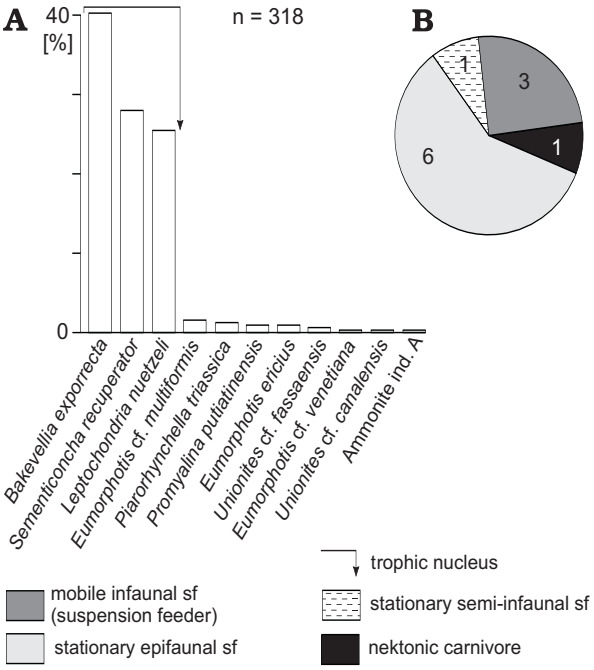

Fig. 12. Characteristics of the *Bakevellia exporrecta* Association showing frequency distribution and trophic nucleus (**A**) and ecological structure (**B**). The numbers in the pie-chart sections correspond with the species pertaining to each guild.

The higher diversity in BD-A-4, which reflects rare occurrences of taxa that typically occur in other faunas, suggests that there might be some time averaging involved (Fürsich and Aberhan 1990). Since the trophic nucleus of both samples is very similar, it can be assumed that the habitats were not fundamentally different. However, the higher portion of epibyssate bivalves in the sample BD-A-4 may result from more firm substrate conditions provided by the limestone bed in which the fossils were observed. In contrast, BD-A-6 is exclusively derived from a shaly interval, which originally provided poorly consolidated substrate conditions. This interpretation is supported by the high numerical abundance of semi-infaunal (*B. exporrecta*) and infaunal (*Sementiconcha recuperator*) bivalves in the trophic nucleus of this sample.

***Eumorphotis ericius* Association**.—This association (Fig. 13) is recorded by the samples BD-A-5, BD-A-7, and VR-1 and comprises the most diverse faunas. The trophic nucleus is represented by epifaunal bivalves (*Eumorphotis ericius, Eumorphotis* cf. *multiformis, Promyalina putiatinensis*, and *Leptochondria nuetzeli*), epifaunal brachiopods (*Protogusarella smithi*), semi-infaunal bivalves (*Bakevellia exporrecta* and *Bakevellia costata*) and sponges (*Cypellospongia* sp. A). In all samples of this assemblage, echinoderms are very common (*Holocrinus smithi* and *Miocidaris utahensis*). Species

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richness ranges from 7 to 15 (mean average = 10). The dominance is low and ranges from 0.16 to 0.29 (mean average = 0.21). This association is exclusively recorded in thin to medium bedded limestone of the lower shoreface to proximal offshore transition zone. Specimen size of the shelly fauna is, in general, highly variable, which suggests that the samples are unaffected by size sorting or alteration by waves or currents. Bivalve shells are usually separated, but very little fragmentation and the lack of graded bedding points to negligible reworking by storms. These taphonomic characteristics and the relatively high species-overlap among individual samples suggest that this association records an autochthonous to para-autochthonous community. The beds recording this assemblage are composed of slightly siliclastic limestone, which was deposited in the inner and proximal outer shelf zone. Ecologically, this fauna is dominated by stationary, attached epifaunal and infaunal suspension feeders, which points to a soft but consolidated substrate. Although represented by few species with a rather low abundance, most other trophic groups of the Virgin fauna are recorded within this association, indicating unstressed ecological conditions. The high diversity and the presence of stenohaline organisms (echinoderms and sponges) suggest normal, fully marine conditions.

***Protogusarella smithi* Association**.—A high diversity association (Fig. 14) is recorded by the samples BD-A-3, BD-B-1, BD-B-0, and VR-2, which is characterised by high abundances of epifaunal brachiopods (*Protogusarella smithi*, *Piarorhynchella triassica*) and epifaunal bivalves (*Eumorphotis ericius* and *Promyalina putiatinensis*). A semi-infaunal bivalve species (*Bakevellia exporrecta*) is locally abundant. The faunal composition of this association is quite heterogeneous, and many of the bivalve and gastropod species recorded in the Virgin Formation are spread within these samples. Debris of echinoderms is very frequent. Species richness ranges from 5 to 13 (mean average 10). This association shows comparably low dominance values (0.18–0.53, mean average 0.28). Similar to the *Eumorphotis ericius* Association, this fauna shows little evidence for reworking and, thus, is herein considered to record a palaeocommunity. The ecological structure is also very similar to the *Eumorphotis ericius* Association, but the dominance of epifaunal suspension feeders is much higher due to the high abundance of the brachiopods *Protogusarella smithi* and *Piarorhynchella triassica* in the sample BD-B-1. The sedimentological framework of this fauna is comparable to that of the previous association, but the somewhat higher thicknesses and the position within the sections indicate that the beds containing this fauna were deposited in slightly shallower waters with more persistent high current velocities.

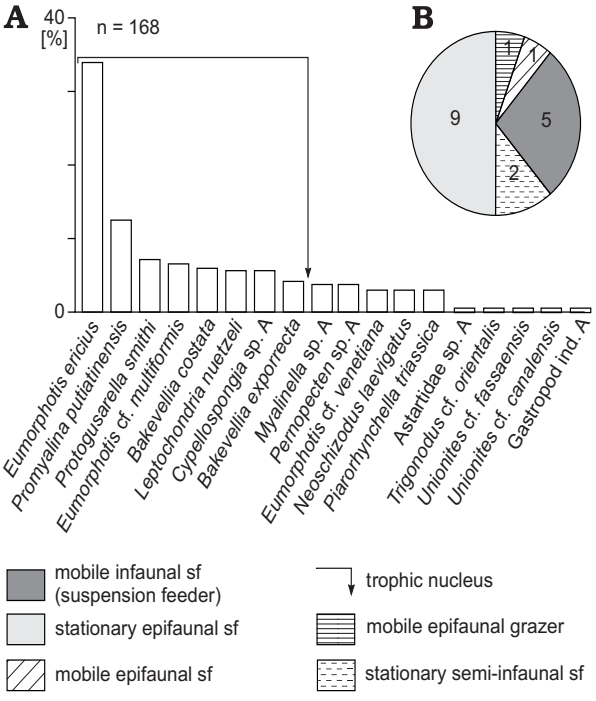

Fig. 13. Characteristics of the *Eumorphotis ericius* Association showing frequency distribution, trophic nucleus (**A**) and ecological structure (**B**).The numbers in the pie-chart sections correspond with the species pertaining to each guild.

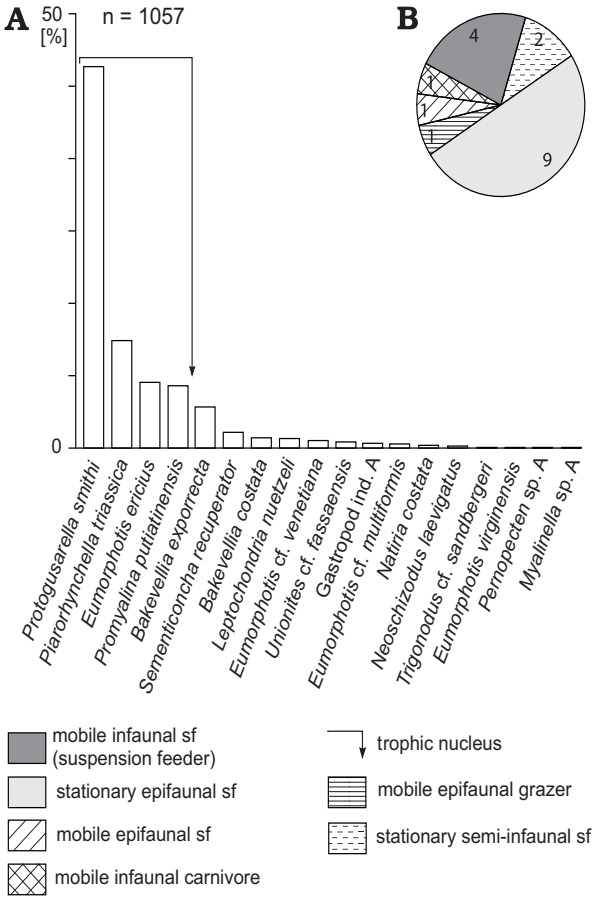

Fig. 14. Characteristics of the *Protogusarella smithi* Association showing frequency distribution, trophic nucleus (**A**) and ecological structure (**B**). The numbers in the pie-chart sections correspond with the species pertaining to each guild.

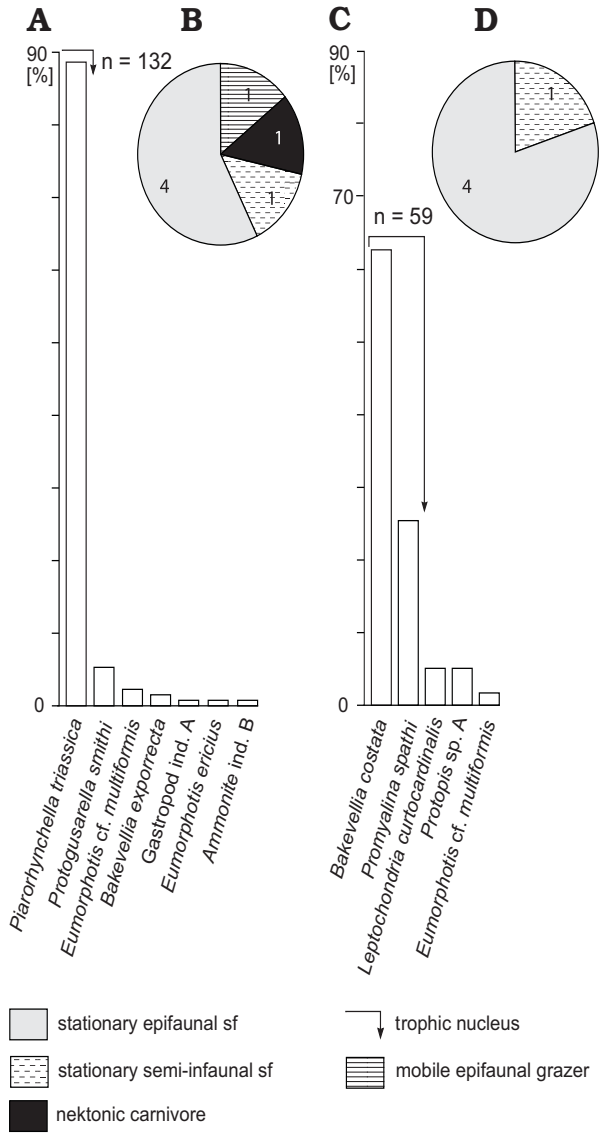

Fig. 15. **A**, **B**. Characteristics of the *Piarorhynchella triassica* Association showing frequency distribution, trophic nucleus (**A**) and ecological structure (**B**). **C**, **D**. Characteristics of the *Bakevellia costata* Assemblage showing frequency distribution and trophic nucleus (**C**) and ecological structure (**D**). The numbers in the pie-chart sections correspond with the species pertaining to each guild.

Abundant echinoderm fragments point to normal marine conditions.

***Piarorhynchella triassica* Association**.—This association (Fig. 15A, B) is represented by the samples HC-C-1 and HC-B-1 and yields epifaunal brachiopods (*Piarorhynchella triassica* and *Protogusarella smithi*) as the most dominant elements. In only one sample, some epifaunal bivalves are recorded in low numbers. Species richness is between 2 and 7 (mean 3.5). Dominance is highest in these samples (0.68–0.82, mean 0.75). *P. triassicia* is frequently observed in life position, indicating that this element of the community is largely autochthonous. Other faunal elements are relatively rare, but the prevalence of complete shells suggests that they were transported over short distances or lived near this habitat. This association is exclusively recorded in calcareous foreshore and tidal inlet deposits. The high dominance most likely reflects the high abiotic stress which is provided by persisting currents in very shallow waters.

***Bakevellia costata* Assemblage**.—This assemblage (Fig. 15C, D), dominated by a semi-infaunal bivalve (*Bakevellia costata*), is represented by one sample only, with a quite unique composition comprising epifaunal bivalves (*Promyalina spathi, Protopis* sp., and *Leptochondria curtocardinalis*) observed in this bed only. Richness is low (5 species) and dominance is moderate (D = 0.46). The ecological structure of this community is very simple, with two trophic guilds present. Echinoderms were not observed. This fauna is recorded in marlstone beds with densely packed specimens, and the sedimentary facies is difficult to interpret. Adjacent strata (upper part of section HC-D) point to a marginal marine environment (see depositional environment HC-D on p. 163). The shells are not oriented, and sizes are variable, which suggests that the fauna is not highly reworked or sorted by currents. However, since this assemblage is represented by a single sample, it contributes only little data, and its low diversity should not be overemphasised.

Results of the R-mode cluster analysis (grouping of species).—The grouping of species roughly indicates which taxa have similar occurrence patterns in a set of samples. Although this information is of lesser significance for community analysis than the Q-mode algorithm (Gahr 2002), it can help to refine the interpretation of sample associations (e.g., Ludvigsen and Westrop 1983; Brinkman et al. 2004). As presented in Fig. 11, some groups can be recognised. Branches that comprise only one taxon but are well separated yield almost no information, because this just reflects the very rare occurrence of this species. A group of two or more taxa largely delineates joint occurrences with similar abundances. An apparent pattern which can be deduced from Fig. 11 is that two sets of taxa seem to be readily distinguishable. The first contains *Bakevellia exporrecta*, *Leptochondria nuetzeli*, and *Sementiconcha recuperator* (Fig. 11G) and the second *Eumorphotis ericius*, *Protogusarella smithi*, *Piarorhynchella triassica*, and *Promyalina putiatinensis* (Fig. 11H). The latter is, in particular, recorded by those associations which were found in high-energy, near-shore deposits (Fig. 11B–D). Accordingly, this cluster unites suspension feeding taxa that are adapted to high water turbulence. In contrast, the cluster dominated by *Bakevellia exporrecta* primarily constitutes the *Bakevellia exporrecta* Association, which is found in environments recording quiet water conditions. It is therefore not surprising that most clusters more or less reproduce the trophic nuclei of associations (Fig. 11G–H). However, the clusters subsumed under Fig. 11F are not well resolved, with rather short stems and high similarities within these clusters. This suggests that these taxa are relatively unspecialised, which, by approximation, is

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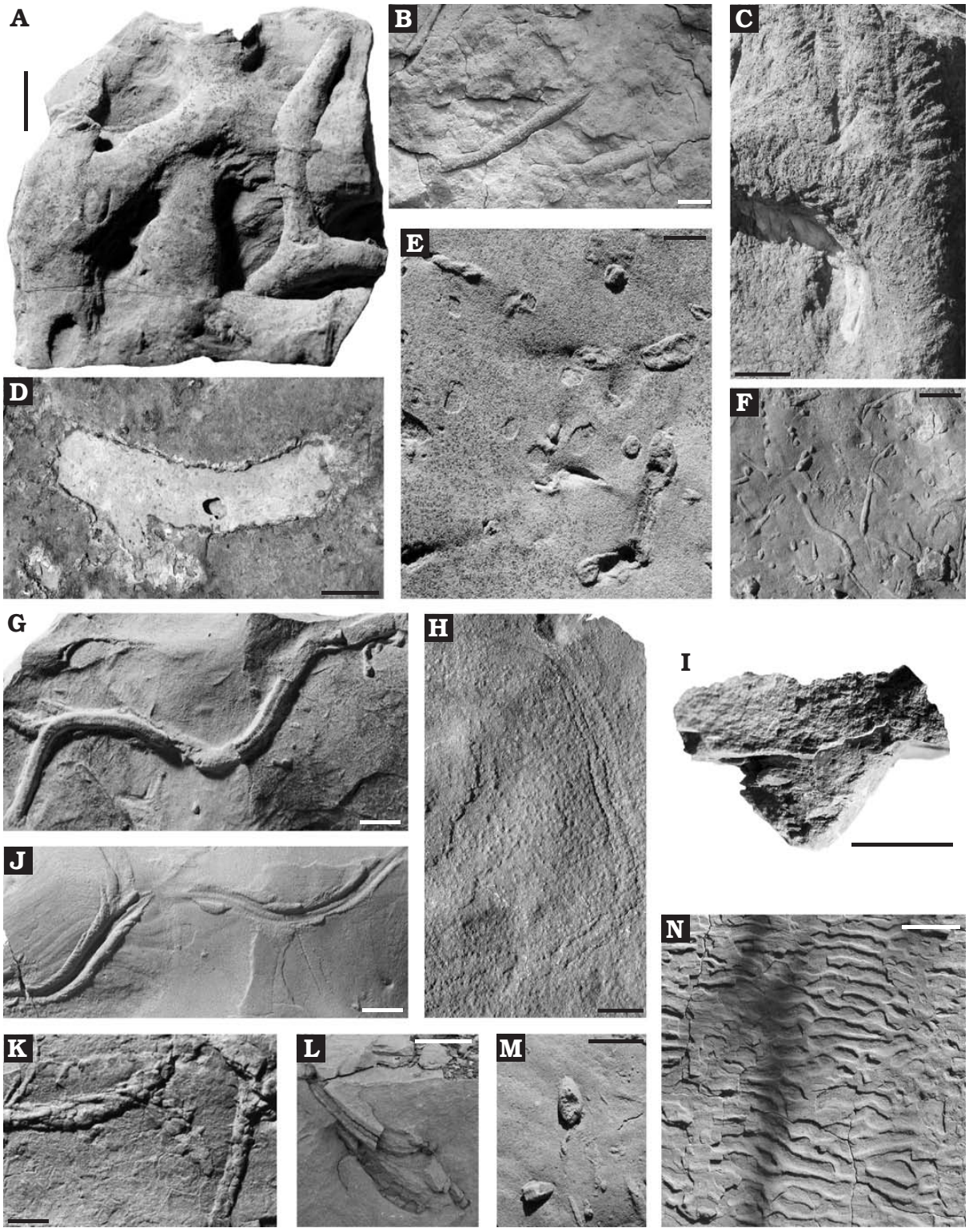

Fig. 16. Trace fossils of the Spathian, Lower Triassic Virgin Formation. **A**. *Thalassinoides* cf. *suevicus* Rieth, 1932 in lower bedding plane view found at the base of beds containing sample BD-A-7, PIMUZ29586. **B**. *Palaeophycus montanus* Hall, 1847 in upper bedding plane view observed the lower calcareous unit of section HC-A. **C**. *Spongeliomorpha* isp. found at the base of grainstone which represents a lateral equivalent of BD-A-7 in the section BD-C. →

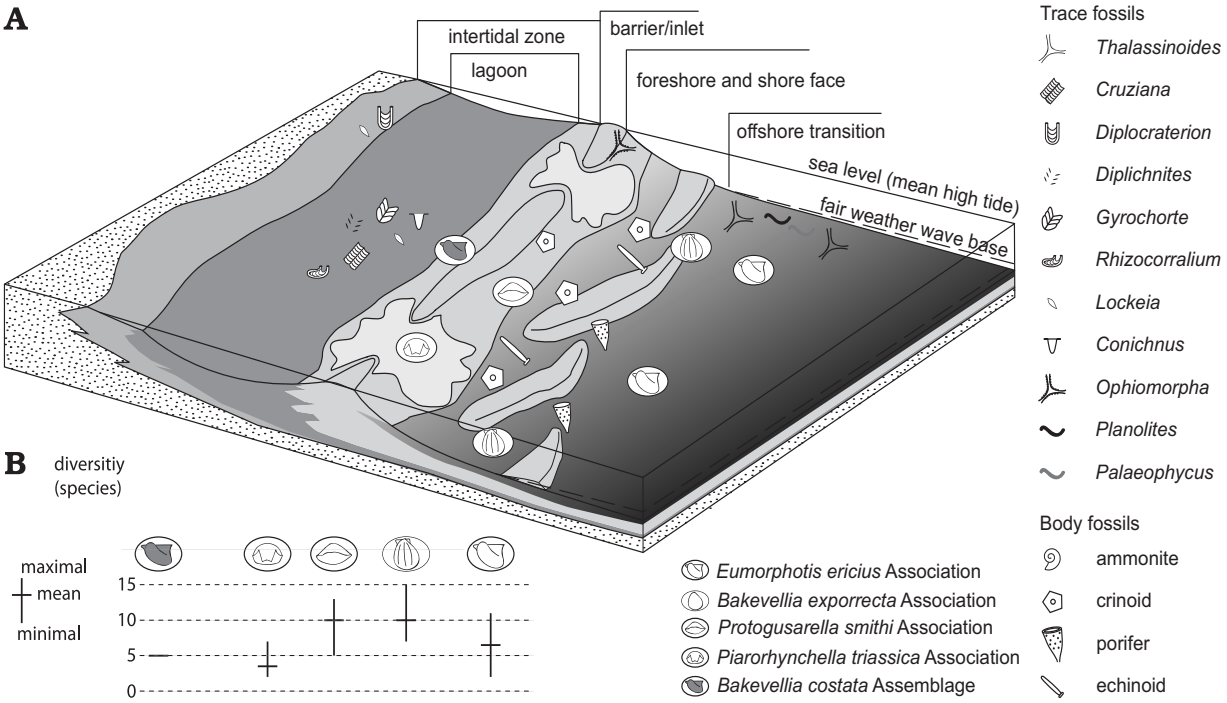

Fig. 17. Comprehensive model of the Spathian (Lower Triassic) Virgin Formation as recorded in south-western Utah. **A**. Distribution of sedimentary facies and faunal assemblages. **B**. Diversity gradient along the general environmental gradient.

expressed in the groupings of samples obtained by the Q-mode cluster analysis. Another possibility is that shared Q-mode occurrences of distant R-mode clusters represent time averaging and community palimpsesting, respectively. The sample BD-A-3 could represent such a case, where the core of two communities is recorded in one bed, because both clusters seem to dominate this sample to a similar extent. The combined analysis of Q- and R-mode clustering thus potentially enables to detect time averaging and community mixing, which is otherwise difficult to deduce unequivocally from sedimentologic and taphonomical criteria alone (Fürsich and Aberhan 1990).

Biological sedimentary structures.—A comprehensive review of the trace fossils is beyond the scope of this study, but they are mentioned because some forms were not reported in earlier studies (e.g., Pruss and Bottjer 2004; Mata and Bottjer 2011) and they are useful for testing sedimentologic and ecological interpretations. Most trace fossils are recorded in siliclastic intervals. All ichnofossils encountered in the field are listed in the Table 1 and are illustrated in Fig. 16. Their stratigraphic occurrences are shown Figs. 4 and 7. Their principal facies occurrences are included in the Fig. 17A and briefly reviewed in the following as loosely defined ichnoassemblages (sensu Bromley 1996).

Open marine ichnoassemblage.—This assemblage is observed in intervals that record shoreface and shallow subtidal environments and largely corresponds with the environmental range of the *Eumorphotis ericius* and the *Protogusarella smithi* Association. *Thalassinoides* cf. *suevicus* (Fig. 16A), *Palaeophycus tubularis* (Fig. 16B), *Spongeliomorpha* isp. (Fig. 16C), and *Planolites montanus* are predominantly recorded in more distal deposits of the lower shoreface and upper offshore transition zone. Although exhibiting a relatively simple structure and comparably low diversity, the dominance of infaunal deposit feeding structures in this assemblage roughly corresponds with the characteristics of a depauperate *Cruziana* ichnofacies (McIlroy 2004), which supports the sedimentologic interpretation. In the near shore high energy facies, *Ophiomorpha* (Fig. 16D) is occasionally observed, which agrees well with sedimentologic interpreta-

This specimen shows a cruzianid scratchpattern similar to that observed in *Cruziana seilacheri* Zonneveld, Pemberton, Saunders, and Pickerill, 2002). **D**. *Ophiomorpha* isp. from uppermost calcareous beds of section HC-A. **E**. *Diplocraterion* isp. in upper bedding plane view. Upper siliclastic interval of BD-B. **F**. *Lockeia siliquaria* James, 1879 showing intergradation with very indistinct locomotion tracks of the same tracemaker. Intertidal interval of section BD-A. **G**. *Cruziana problematica* Schindewolf, 1928 from the lagoonal siltstone interval of section HC-D, PIMUZ29606. **H**. *Diplichnites* isp. from the lagoonal siltstone interval of section HC-D. **I**. *Conichnus* isp. from the lagoonal siltstone interval of section HC-A, PIMUZ29607. **J**. Arthropod trackway (cf. *Diplopodichnus* intergrading with *Diplichnites*) from the lagoonal siltstone interval of section HC-D, PIMUZ29605. **K**. *Gyrochorte* cf. *comosa* Heer, 1865 from the lagoonal siltstone interval of section HC-A, PIMUZ29608. **L**. *Rhizocorallium* isp. from the lagoonal siltstone interval of section HC-A. **M**. *Lockeia siliquaria* James, 1879 from the lagoonal siltstone interval of section HC-D. **N**. Wrinkle marks from the lagoonal siltstone interval of section HC-D. Scale bars 10 mm; except C, H, N, 20 mm; F, 30 mm.

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tion and delineates a low diverse *Skolithos* ichnofacies (McIlroy 2004). These open marine assemblages suggest that an environmental gradient is faintly mirrored in the ichnotaxonomic composition, making the ichnofacies concept (Seilacher 1967) applicable in the Virgin Formation.

Intertidal ichnoassamblage.—This assemblage is observed in the tidal flat facies recorded in the upper part of the Beaver Dam sections (BD-A, BD-B, and VR; Fig. 4). It contains the trace fossils *Diplocraterion* isp. (Fig. 16E) and *Lockeia siliquaria* (Fig. 16F). The low diversity of this assemblage possibly reflects the high rate of abiotic stress to which biota are subjected in such environments. However, the paucity of ichnotaxa could also result from very limited exposures of this facies in the Virgin Formation.

Lagoonal ichnoassemblage.—This assemblage is observed in the lagoonal intervals identified in the section HC-A and HC-D and includes the trace fossils *Lockeia siliquaria* (Fig. 16M), *Cruziana problematica* (Fig. 16G), *Gyrochorte* cf. *comosa* (Fig. 16K), *Conichnus* isp. (Fig. 16J), *Diplichnites* isp. (Fig. 16H), *Rhizocorallium* isp. (Fig. 16L), *Diplocraterion* isp. and an arthropod trackway which could be referred to an intergradational form of *Diplopodichnus* and *Diplichnites* (Fig. 16I). Furthermore, wrinkle structures (Fig. 16N) are recorded in some of beds of this facies. This is the most diverse trace fossil assemblage, which most likely reflects the high content of siliclastic material, alternating grain sizes, and modest sedimentation rates. These characteristics provide a high preservation potential for trace fossils. In protected marginal marine embayments, the rate of bioturbation is highly variable (Mángano and Buatois 2004), which is seen in our data as well. The generally low rate of biogenic mixing could result from local stress factors in marginal marine settings such as high water temperatures, salinity fluctuations and poor mixing of the water body. These shale beds are devoid of marine body fossils, which are recorded in otherwise similar deposits of the offshore transition (e.g., BD-A-6).

Controls on the distribution and ecological structure of the Virgin Fauna.—Based on the sedimentological data and palaeoecological analysis outlined above, a model of the palaeoecological conditions recorded by the Virgin Formation can be inferred (Fig. 17A). All assemblages record marine conditions in a shallow water environment with relative water depths not ranging below the storm wave base. Main trends in diversity, dominance and trophic complexity are chiefly controlled by substrate conditions and hydrodynamic regime.

The *Bakevellia exporrecta* Association is present in the most distal marine facies recorded in the study area. As already noted, its rather low diversity and modest dominance probably reflects soft substrate conditions, which are unfavourable for attached, epifaunal bivalves that otherwise represent the major faunal elements in the Virgin Formation and generally, in Early Triassic benthic ecosystems. The carbonate-dominated units of the inner shelf environment (or shoreface zone) of the Virgin Formation contain the most diverse and ecologically most heterogeneous associations. Their distribution seems to roughly follow an environmental gradient that is largely controlled by hydrodynamic regime. The *Eumorphotis ericius* Association is present in the most distal parts of the shoreface zone and probably the proximal offshore transition. This is the only facies where sponges are abundant. The *Piarorhynchella triassica* Association probably represents somewhat shallower water depths, which can be inferred from the sedimentological context of these samples, including medium-to-thick-bedded as well as cross-bedded grainstone units. The highest energy deposits of very shallow subtidal and probably intertidal conditions, which are represented by tidal inlet and tidal channel deposits, host the *Piarorhynchella triassica* Association, which is chiefly dominated by this rhynchonellid brachiopod. All of these associations contain abundant crinoid fragments indicating normal marine, well oxygenated, current agitated waters with low siliclastic input. The sedimentological context (see last paragraph on the sedimentary environment of HC-D on p. 163) of the *Bakevellia costata* Assemblage suggests a very marginal setting.

Although epifaunal suspension feeders are the main constituents of the Virgin Fauna, the general trophic structure with guilds represented by body fossils and three additionally inferred from trace fossils (Table 1) indicate that the ecological diversity is comparably advanced and not fundamentally different from later Mesozoic shallow marine habitats (see Aberhan 1994).

Discussion

A delayed recovery?—Our study confirms the comparably high bulk diversity of benthic taxa in the Virgin Formation (McGowan et al. 2009; Hautmann et al. 2012), to which it adds one more genus (*Myalinella*), the presence of the family Astardidae, and one more species (*Promyalina spathi*), resulting in the highest bivalve diversity (30 species, 18 genera) of any formation from the Early Triassic reported so far and considerably exceeding the ten bivalve genera identified in earlier studies (e.g., Schubert and Bottjer 1995). Although the individual sample diversity observed by Schubert and Bottjer (1995) is similar on the generic level, these authors noted that the Spathian communities still show a simple ecological structure containing mainly generalistic taxa, which led to the conclusion that the recovery was significantly delayed throughout the Early Triassic. However, the bivalve diversity of the Virgin Formation is not so different from that of similar settings from the Middle Triassic post-extinction radiation interval of bivalves in different areas, for instance in Vietnam (28 species and 19 genera for the Anisian and Ladinian; Komatsu et al. 2010) and the Dolomites (15 genera for the early Anisian, 32 genera for the late Anisian; Posenato 2008). Bivalve diversity was higher in the middle Anisian Jena Formation (lower Muschelkalk) of the Germanic

Basin (57 species and 30 genera; Schmidt 1928, 1938), but McGowan et al. (2009) suggested that this may partly reflect its longer study history, the longer duration of the time interval recorded and the larger outcrop area. This view is supported herein by finds of additional bivalve taxa (*Myalinella* sp., Astardidae sp., *Promyalina spathi)* that were not identified by McGowan et al. (2009) and Hautmann et al. (2012) in the same area, although the overall richness as reported in these studies was not achieved herein. This suggests that, at least to some extent, the lower bulk diversity of the Virgin Formation in comparison with well studied Middle Triassic faunas reflects lower sampling effort.

Summarized, bivalve diversity of the Virgin Formation is more similar to faunas from comparable settings of Anisian age than to pre-Spathian faunas of the Early Triassic, suggesting that significant recovery has already taken place. This does not imply that recovery was already completed by that time, as shown by the extraordinary diverse bivalve fauna from the Late Anisian Leidapo Member in China (103 species, 49 genera; Stiller 2001). However, the relatively high diversity, the appearance of other typical Mesozoic benthic organisms such as articulated brachiopods, porifers, echinoderms, and the presence of certain ichnotaxa that indicate advanced recovery stages (Twitchett and Wignall 1996; Hofmann et al. 2011) suggest that recovery was already underway in the Early Spathian, contrary to earlier studies on the Virgin Formation (e.g., Schubert and Bottjer 1995; Boyer et al. 2004; Pruss and Bottjer 2004; Mata and Bottjer 2011).

Harsh environmental conditions?—The benthic associations of the Virgin Formation in the investigated area reflect normal marine conditions. Deleterious environmental conditions, caused, for example, by the upwelling of anoxic and alkaline waters (Mata and Bottjer 2011), are not confirmed because the taxonomic composition does not change between different stratigraphic levels and thus indicates the absence of faunal turnovers, which would one expect in case of discrete environmental perturbations. The reduced diversity and high dominance of the faunas recorded by the *Bakevellia exporrecta* Association and the *Piarorhynchella triassica* Association are most likely related to substrate properties and hydrodynamic conditions as well as taphonomic bias possibly introduced by sorting (*Piarorhynchella triassica* Association). Alternatively, this pattern could be interpreted by the "habitable zone" concept of Beatty et al. (2008). In this model, onshore habitats remain oxygenated by wave action and thus may have served as refuges for benthic biota to escape from oxygen deficiency in open oceanic settings. However, all observed genera that occur in the most distal deposits within the study area (*Bakevellia exporrecta* Association) are not diagnostic for oxygen restricted habitats. *Bakevellia* has frequently been documented from oxygenated, shallow marine habitats (e.g., Aberhan 1992; Muster 1995; Fürsich et al. 1995; Aberhan and Muster 1997). *Leptochondria*, ranging from the late Permian to the Norian, is also known occur in well oxygenated deposits such as the Middle Triassic Muschelkalk (Schmidt 1928). The presence of infaunal bivalves (*Sementiconcha recuperator*) additionally argues against a notably impact of anoxic or hypoxic ocean waters. Furthermore, the presence of *Thalassinoides*, *Ophiomorpha,* and *Spongeliomorpha* points to well oxygenated conditions (Savrda and Bottjer 1986) throughout all environmental settings recorded by the Virgin Formation in the investigated area.

Comparison with other Spathian benthic faunas.—Very few studies on Spathian faunas from other palaeogeographic regions are available for comparison. 30 benthic species (19 genera) are reported from the uppermost Werfen Formation (Cencenighe and San Lucano members) of the Dolomites (Neri and Posenato 1985). Broglia-Loriga et al. (1990) observed 23 benthic species (17 genera) in the Spathian part of the Werfen Formation, and 19 species (16 genera) in the palaeogeographically closely related Transdanubian Mountains (Hungary). Both studies document a similar taxonomic composition to the Virgin fauna, at least with respect to the mollusc genera. Furthermore, it has been suggested that the Olenekian part of the Werfen Formation marks the initial recovery phase succeeding a surviving phase in the Induan (Posenato et al. 2008). In fact, Werfen faunas reached their highest diversity in the Spathian (Broglia-Loriga et al. 1990; Posenato 2008; personal observation RH and MH). Similarly, Twitchett and Wignall (1996) noted that the ichnofaunas of the Werfen Formation show the highest stage of recovery in the Spathian. All these data suggest that the recovery signal observed in the western USA is of interregional significance. Faunal differences between the western USA and the Alps include the local dominance of articulated brachiopods and the presence of porifers in the Virgin Formation, which are not observed in the Werfen Formation. However, sponge build-ups were reported in the western Tethys realm (Szulc 2007), which adds further evidence for similar recovery patterns on either coast of Pangaea (Brayard et al. 2011b).

Data from other palaeogeographic regions are scarce, and comparable palaeoecological surveys were not presented, yet. Bivalve faunas from a southern Tethyan succession (Pakistan) yield 14 Spathian species (11 genera) (Wasmer et al. 2012) with a somewhat different taxonomic composition, possibly indicating increasing faunal provincialism. Future studies are necessary to further clarify the picture of benthic recovery and possible migration patterns of benthic species.

Habitat differentiation and a new ecological recovery model.—In spite of the relatively high bulk diversity observed in the Virgin Formation, the taxonomical differentiation between adjoining habitats and along environmental gradients is surprisingly low (Figs. 11, 17). In fact, the benthic associations identified as clusters (Fig. 11) largely reflect the variable dominance of certain taxa, whereas differences in the taxonomic composition are of minor importance. Those taxa that are unique to associations are recorded in very small numbers, which probably indicates sampling bias rather than notable taxonomic differences. Low bootstrap values (Fig. 11) addi-

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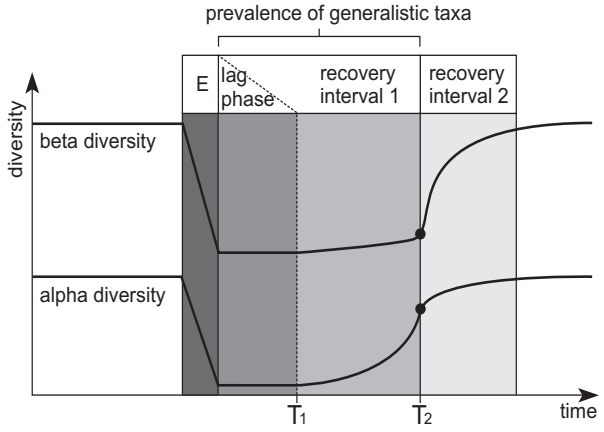

Fig. 18. Generalised model illustrating the role of habitat saturation in recovery processes. Following the extinction (E), a lag phase marks a time interval in which no significant radiation and increase in alpha diversity is observed (Ewin 2001). The duration of this lag phase may be variable or it could even be absent (Hautmann et al. 2008) but it is commonly postulated for the end-Permian mass extinction (e.g., Erwin 2001). After initiation of diversification (T_1, start of recovery interval 1), competition within habitats increases following recovering alpha diversity. Beta diversity remains low throughout this interval because adding new species does not yet result in significant competition for resources. Eventually, alpha diversity reaches a threshold value where a critical number of species competes for same, limited resources. The time when this habitat saturation is reached is herein referred to as T_2. From this time onward (recovery interval 2), habitat restriction increases because of competitive exclusion of species from neighbouring habitats. Recovery interval 2 ends when all curves level off. Logistic growth of alpha diversity adopted from Erwin (2001).

tionally suggest that the groupings obtained in the Q-mode clustering reflect only minor differences between associations, chiefly caused by variable abundances of taxa. If confirmed by future studies in other regions, this pattern would indicate a time lag between increasing habitat diversity (alpha diversity) and increasing taxonomical differentiation between habitats (beta diversity), contrary to the expectations of Whittaker (1975). We hypothesise that competition, roughly expressed as the average number of species in a set of habitats, needs to exceed a certain threshold before taxonomical differentiation between habitats starts, and that this threshold was not yet reached in the Early Spathian of the investigated area. Accordingly, a significant increase in beta diversity could be used to divide recovery intervals into two major phases, the first ending with reaching a habitat saturation threshold and the second ending with the completion of ecosystem differentiation, indicated by the end of an increase in beta diversity.

The herein proposed model (Fig. 18) is in accordance with the niche overlap theory of Pianka (1974), which predicts decreasing niche overlap with increasing number of competing species and a corresponding increase of diffuse competition sensu MacArthur (1972). The existence of a competition threshold before significant taxonomic differentiation along an environmental gradient starts is not part of the theory of Pianka (1974), but it is compatible with standard models of interspecific competition with a prevalence of diffuse competition. In this situation, an increase of the number of competing species i in a given habitat will lead to exclusion of a species j from this habitat when the sum of $\alpha_{ij}N_i$ (α, competition coefficient; N, equilibrium abundance) has exceeded the threshold where $N_j < 0$ for the equilibrium condition of the multi-species Lotka-Volterra equation (e.g., Pianka 1974: equation 2).

Our findings somewhat contradict the interpretation of ANOSIM (analysis of similarity) analyses presented by McGowan et al. (2009), who suggested that the Virgin Fauna is comparatively heterogeneous. A detailed comparison of the different methods (cluster analysis versus ANOSIM) is beyond the scope of this paper, but when running cluster analyses with the dataset of McGowan et al. (2009) we obtained similar results as in our study. In particular, well separated clusters of samples (associations) identified in the dataset of McGowan et al. (2009) contain few or no taxa that are truly unique to these associations, similar to the results of our study. The difference in the interpretation may simply result from different views of what should be called "heterogeneous", but we note that the R-values presented by McGowan et al. (2009: table 4) are all close to zero, with subtle differences that indicate a low heterogeneity with respect to facies gradients and stratigraphic levels.

Our interpretation is an alternative to the hypothesis that the prevalence of generalistic taxa in the Early Triassic reflects protracted environmental stress, which has been advocated in recent studies on the Virgin Formation (e.g., Pruss and Bottjer 2004; Boyer et al. 2004; Mata and Bottjer 2011). Our results rather support the view of Schubert and Bottjer (1995: 28) that the generalistic character of Spathian faunas of the western USA largely reflects intrinsic controls, which we identified as relatively low levels of competition among species within most habitats. Future studies on Early Triassic and Middle Triassic benthic communities of different environments are necessary to test the proposed model.

Conclusions

The quantitative palaeoecological analysis of the Virgin Formation in south-western Utah yields the following main conclusions:

- The Virgin Formation contains the taxonomically and ecologically most diverse benthic fauna in the Early Triassic aftermath of the end-Permian mass extinction.
- Relatively small differences in the taxonomic composition and abundances data led to the recognition of four associations and one assemblage, delineating an environmental gradient ranging from intertidal to subtidal habitats.
- Comparably low diversities in some associations were chiefly caused by hydrodynamic conditions and substrate properties.
- Unusual environmental conditions were not found to have had any significant impact on benthic ecosystems recorded by the Virgin faunas. This suggests that oceano-

graphic conditions during the Early Spathian enabled ecosystems to re-diversify without major abiotic limitations in the western USA.

- The similarity in the taxonomical composition of individual habitats indicates that the high bulk diversity of the Virgin Fauna was mainly achieved by the pan-environmental establishment of species. This generalistic nature of biota probably reflects low levels of competition rather than stressful environmental conditions.
- The onset of increasing taxonomical differentiation between habitats is a potential indicator of the relative state of ecosystem recovery after mass extinction events.

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References

Aberhan, M. 1992. Palökologie und zeitliche Verbreitung benthischer Faunengemeinschaften im Unterjura von Chile. *Beringeria* 5: 3–174.

Aberhan, M. 1994. Guild-structure and evolution of Mesozoic benthic shelf communities. *Palaios* 9: 516–545.

Aberhan, M. and Muster, H. 1997. Palaeobiology of Lower Jurassic bakevelliid bivalves from western Canada. *Palaeontology* 40: 799–815.

Alberti, F. von 1864. *Überblick über die Trias, mit Berücksichtigung ihres Vorkommens in den Alpen*. 353 pp. J.G. Cottasche Buchhandlung, Stuttgart.

Beatty, T.W., Zonneveld, J.P., and Henderson, C.M. 2008. Anomalously diverse Early Triassic ichnofossil assemblages in Northwest Pangea: a case for a shallow-marine habitable zone. *Geology* 36: 771–774.

Bissell, H.J. 1973. Permian–Triassic boundary in the eastern Great Basin area. *In*: A. Logan, and L.V. Hills (eds.), Permian and Triassic Systems and Their Mutual Boundary. *Canadian Society of Petroleum Geologists Memoirs* 2: 318–344.

Bambach, R.K. 1977. Species richness in marine benthic habitats through the Phanerozoic. *Paleobiology* 3: 152–167.

Bittner, A. 1899. Trias–Ablagerungen des Süd-Ussuri-Gebietes in der ostsibirischen Küstenprovinz. *Mémoires du Comité Géologique* 7: 1–35.

Blakey, R.C. 2011. Colorado Plateau Stratigraphy and Geology and Global and Regional Paleogeography. http://www2.nau.edu/rcb7/index.html. (Accessed February 2011).

Boyer, D.L., Bottjer, D.J., and Droser, M.L. 2004. Ecological Signature of Lower Triassic Shell Beds of the Western United States. *Palaios* 19: 372–380.

Bray, J.R. and Curtis. J.T. 1957. An ordination of upland forest communities of southern Wisconsin. *Ecological Monographs* 27: 325–349.

Brayard, A., Escarguel, G., Bucher, H., Monnet, C., Brühwiler, T., Goudemand, N., Galfetti, T., and Guex, J. 2009. Good genes and good luck: ammonoid diversity and the end-Permian mass extinction. *Science* 325: 1118–1121.

Brayard, A., Nützel, A., Stephen, D.A., Bylund, K.G., Jenks, J., and Bucher, H. 2010. Gastropod evidence against the Early Triassic Lilliput effect. *Geology* 38: 147–150.

Brayard, A., Nützel, A., Kaim, A., Escarguel, G., Hautmann, M., Stephen, D.A., Bylund, K.G. Jenks, J., and Bucher, H. 2011a. Gastropod evidence against the Early Triassic Lilliput effect: REPLY. *Geology* 39: e233.

Brayard, A., Vennin, E., Olivier, N., Escarguel, G., Bylund, K.G., Jenks, J., Stephen, D.A., Hofmann, R., Goudemand, N. and Bucher, H. 2011b. Transient metazoan reefs in the aftermath of the end-Permian mass extinction. *Nature Geoscience*. 4: 693–697.

Brinkman, D.B., Russell, A.P., Eberth, D.A., and Peng, J. 2004. Vertebrate palaeocommunities of the lower Judith River Group (Campanian) of southeastern Alberta, Canada, as interpreted from vertebrate microfossil assemblages. *Palaeogeography, Palaeoclimatology, Palaeoecology* 213: 295–313.

Broglio-Loriga, C., Góczán, F., Haas, J., Lenner, K., Neri, C., Oravecz-Scheffer, A., Posenato, R., Szaboacute, I., and Tóth Makk, A. 1990. The Lower Triassic sequence of the Dolomites (Italy) and Transdanubian Mid-Mountains (Hungary) and their correlation. *Memorie di Scienze Geologiche, Padova* 42: 41–103.

Bromley R.G. 1996. *Trace fossils. Biology, taphonomy and applications.* 361 pp. Chapman and Hall, London.

Catullo, T.A. 1846. Memoria geognostico-paleozoica sulle Alpi Venete. *Memorie della Società Italiana delle scienze residente in Modena* 24: 1–158.

Cheel, R.J. and Leckie, D.A. 1993. Hummocky cross-stratification. *Sedimentology Reviews* 1: 103–121.

Clark, W.B. and Twitchell, M.W. 1915: The Mesozoic and Cenozoic Echinodermata of the United States. *Monographs of the United States Geological Survey* 54: 1–341.

Erwin, D.H. 1993. *The Great Paleozoic Crisis: Life and Death in the Permian*. 327 pp. Columbia University Press, New York.

Erwin, D.H. 2001. Lessons from the past: Biotic recoveries from mass extinctions. *Proceedings of National Academy of Science* 98: 5399–5403.

Fürsich, F.T. and Aberhan, M. 1990. Significance of time-averaging for palaeocommunity analysis. *Lethaia* 23: 143–152.

Fürsich, F.T., Freytag, S., Röhl, J., and Schmid, A. 1995. Palaeoecology of benthic associations in salinity-controlled marginal marine environments: Examples from the Lower Bathonian (Jurassic) of the Causses (southern France). *Palaeogeography, Palaeoclimatology, Palaeoecology* 113: 135–172.

Fraiser, M.L. and Bottjer, D.J. 2005. Fossil preservation during the aftermath of the end-Permian mass extinction: Taphonomic processes and palaeoecological signals. *In*: D.J. Over, J. Morrow, and P.B.Wignall (eds.), Understanding Late Devonian and Permian–Triassic Biotic and Climatic Events: Towards an Integrated Approach. *Developments in Palaeontology and Stratigraphy* 20: 299–311.

Gahr, M.E. 2002. Palökologie des Makrobenthos im Unter-Toarc SW-Europas. *Beringeria* 31: 3–204.

Galfetti, T., Bucher, H., Brayard, A., Hochuli, P.A., Weissert, H., Guodun, K., Atudorei, V., and Guex, J. 2007. Late Early Triassic climate change: Insights from carbonate carbon isotopes, sedimentary evolution and ammonoid paleobiogeography. *Palaeogeography, Palaeoclimatology, Palaeoecology* 243: 394–411.

Goodspeed, T.H. and Lucas, S.G. 2007. Stratigraphy, sedimentology, and sequence stratigraphy of the Lower Triassic Sinbad Formation, San Rafael Swell, Utah. *In:* S.G. Lucas and J.A. Spielmann (eds.), Triassic of the American West. N*ew Mexico Museum of Natural History and Science Bulletin* 40: 91–102.

Guex, J., Hungerbühler, A., Jenks, J.F., O'Dogherty, L., Atudorei, V., Taylor, D.G., Bucher, H., and Bartolini, A. 2010. Spathian (Lower Triassic) ammonoids from western USA (Idaho, California, Utah and Nevada). *Mémoires de Géologie Lausanne* 49: 82.

Hall, J. 1847. *Palaeontology of New York, Vol. I. Natural History of New York, 1*. 338 pp. Van Benthuysen, Albany.

http://dx.doi.org/10.4202/app.2011.0060

Hall, J. and Whitfield, R.P. 1877. Part II. Palaeontology. *In*: C. King (ed.), *Annual Report to the Secretary of War on the U.S. Geological Exploration of the Fortieth Parallel 4*, 198–302. Government Printing Office, Washington.

Hallam, A. 1991. Why was there a delayed radiation after the end-Palaeozoic extinctions? *Historical Biology: An International Journal of Paleobiology* 5: 257–262.

Hammer, Ø., Harper, D.A.T., and Ryan, P.D. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4 (1): 9 p. http://palaeo-electronica.org/2001_1/past/issue1_01.htm

Hammer, Ø. and Harper, D.A.T. 2006. *Paleontological data analysis*. 351 pp. Blackwell, Malden.

Hauer, F. von 1850. Ueber die von Herrn Bergrath W. Fuchs in den Venetianer Alpen gesammelten Fossilien. *Denkschriften der Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse* 2: 109–126.

Hautmann, M. and Nützel, A. 2005. First record of a heterodont bivalve (Mollusca) from the Early Triassic: Palaeoecological significance and implications for the 'Lazarus problem'. *Palaeontology* 48: 1131–1138.

Hautmann, M., Bucher, H., Brühwiler, T., Goudemand, N., Kaim, A., and Nützel, A. 2011. An unusually diverse mollusk fauna from the earliest Triassic of South China and its implications for benthic recovery after the end-Permian biotic crisis. *Geobios* 44: 71–85.

Hautmann, M., McGowan, A.J., Smith, A.B., and Bucher, H. 2012. Bivalves from the Spathian (Early Triassic) of southwestern Utah: Systematics and evolutionary significance. *Journal of Systematic Palaeontology* (published online).

Hautmann, M., Stiller, F., Cai, H., and Sha, J. 2008: Extinction-recovery pattern of level-bottom faunas across the Triassic–Jurassic boundary in Tibet: implications for potential killing mechanisms. *Palaios* 23: 711–718.

Heer, O. 1865. *Die Urwelt der Schweiz*. 622 pp. Friedrich Schultheß, Zürich.

Heydari, E., Arzani, N., and Hassanzadeh, J. 2008. Mantle plume: The invisible serial killer—Application to the Permian–Triassic boundary mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 264: 147–162.

Hofmann, R., Goudemand, N., Wasmer, M., Bucher, H., and Hautmann, M. 2011. New trace fossil evidence for an early recovery signal in the aftermath of the end-Permian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 310: 216–226.

Kier, P.M. 1968. The Triassic echinoids of North America. *Journal of Paleontology* 42: 1000–1006.

Kiparisova, L.D. 1938. Lower Triassic bivalves of the Ussuri region [in Russian]. *Trudy Geologičeskogo Instituta* 7: 197–311.

Klein, G.D. 1971. A sedimentary model for determining paleotidal range. *Geological Society of America Bulletin* 82: 2585–2592.

Komatsu, T., Huyen, D.T., and Huu, N.D. 2010. Radiation of Middle Triassic bivalve: Bivalve assemblages characterized by infaunal and semi-infaunal burrowers in a storm- and wave-dominated shelf, An Chau Basin, North Vietnam. *Palaeogeography, Palaeoclimatology, Palaeoecology* 291: 190–204.

Kreisa, R.D. and Moiola, R.J. 1986. Sigmoidal tidal bundles and other tide-generated sedimentary structures of the Curtis Formation, Utah. *Geological Society of America Bulletin* 97: 381–387.

James, U.P. 1879. Descriptions of new species of fossils and remarks on others from the lower and upper Silurian rocks of Ohio. *The Paleontologist* 1 (3): 17–24.

Lepsius, R. 1878. *Das westliche Südtirol*. 375 pp. Verlag Wilhelm Hertz, Berlin.

Lucas, S.G., Krainer, K., and Milner, A.R.C. 2007. The Type section and age of the Timpoweap Member and the stratigraphic nomenclature of the Triassic Moenkopi Group in Southwestern Utah. *In*: S.G. Lucas and J.A. Spielmann (eds.), Triassic of the American West. N*ew Mexico Museum of Natural History and Science Bulletin* 40: 109–118.

Ludvigsen, R. and Westrop, S.R. 1983. Trilobite biofacies of the Cambrian–Ordovician boundary interval in northern North-America. *Alcheringa* 7: 301–319.

MacArthur R.H. 1972. *Geographical Ecology*. 269 pp. Harper and Row, New York.

Mángano, M.G. and Buatois, L.A. 2004. Ichnology of Carboniferous tide-influenced environments and tidal flat variability in the North American Midcontinent. *Geological Society, London, Special Publications* 228: 157–178.

Mansfield, G.R. 1927. Geography, geology, and mineral resources of part of southeastern Idaho. *U.S. Geological Survey Professional Papers* 152: 1–453.

Mata, S.A. and Bottjer, D.J. 2011. Origin of Lower Triassic microbialites in mixed carbonate-siliciclastic successions: Ichnology, applied stratigraphy, and the end-Permian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 300: 158–178.

McGowan, A.J., Smith, A.B., and Taylor, P.D. 2009. Faunal diversity, heterogeneity and body size in the Early Triassic: testing post-extinction paradigms in the Virgin Limestone of Utah, USA. *Australian Journal of Earth Sciences: An International Geoscience Journal of the Geological Society of Australia* 56: 859–872.

McIlroy, D. 2004. Some ichnological concepts, methodologies, applications and frontiers. *Geological Society, London, Special Publications* 228: 3–27.

Morisita, M. 1959: Measuring of interspecific association and similarity between communities. *Memoires of the Faculty of Science, Kyushu University, Series E. Biology* 3: 65–80.

Mundil, R., Ludwig, K.R., Metcalfe, I., and Renne, P.R. 2004. Age and Timing of the Permian Mass Extinctions: U/Pb Dating of Closed-System Zircons. *Science* 305: 1760–1763.

Münster, G. Graf zu 1841. *Beiträge zur Petrefacten-Kunde. IV. Beschreibung und Abbildung der in den Kalkmergelschichten von St. Cassian gefundenen Versteinerungen*. 152 pp. Buchner'sche Buchhandlung, Bayreuth.

Muster, H. 1995. Taxonomie und Paläobiogeographie der Bakevelliidae (Bivalvia). *Beringeria* 14: 1–161.

Myrow, P.M. 1992. Pot and gutter casts from the Chapel Island Formation, Southeast Newfoundland. *Journal of Sedimentary Research* 62: 992–1007.

NACSN (North American Commission on Stratigraphic Nomenclature). 2005. North American stratigraphic code. *AAPG Bulletin* 89: 1547–1591.

Neri, C. and Posenato, F. 1985. New biostratigraphical data on uppermost Werfen Formation of western Dolomites (Trento, Italy). *Geologisch-Paläontologische Mitteilungen Innsbruck* 14: 83–107.

Newell, N.D. and Kummel, B. 1942. Lower Eo-Triassic stratigraphy, western Wyoming and southeast Idaho. *GSA Bulletin* 53: 937–995.

Neyman, A.A. 1967. Limits to the application of the 'trophic group' concept in benthic studies. *Oceanology, Academy of Sciences of the USSR* 7: 49–155.

Ovtcharova, M., Bucher, H., Schaltegger, U., Galfetti, T., Brayard, A., and Guex, J. 2007. New Early to Middle Triassic U–Pb ages from South China: Calibration with ammonoid biochronozones and implications for the timing of the Triassic biotic recovery. *Earth and Planetary Science Letters* 243: 463–475.

Perry, D.G. and Chatterton, B.D.E. 1979. Late Early Triassic brachiopod and conodont fauna, Thaynes Formation, southeastern Idaho. *Journal of Paleontology* 53:307–319.

Pianka E.R. 1974. Niche Overlap and Diffuse Competition. *Proceedings of National Academy of Science* 71: 2141–2145.

Poborski, S.J. 1954. Virgin Formation (Triassic) of the St. George, Utah, Area. *Geological Society of America Bulletin* 65: 971–1006.

Posenato, R. 2008. Patterns of bivalve biodiversity from Early to Middle Triassic in the Southern Alps (Italy): Regional vs. global events. *Palaeogeography, Palaeoclimatology, Palaeoecology* 261: 145–159.

Pruss, S.B., Corsetti, F.A., and Bottjer, D.J. 2005. The unusual sedimentary rock record of the Early Triassic: A case study from the southwestern United States. *Palaeogeography, Palaeoclimatology, Palaeoecology* 222: 33–52.

Pruss, S.B. and Bottjer, D.J. 2004. Early Triassic trace fossils of the western

United States and their implications for prolonged environmental stress from the end-Permian mass extinction. *Palaios* 19: 551–564.

Pruss, S.B. and Payne, J.L. 2009. Early Triassic microbial spheroids in the Virgin Limestone Member of the Moenkopi Formation, Nevada, USA. *Palaios* 24: 131–136.

Pruss, S.B., Payne, J.L., and Bottjer, D.J. 2007. *Placunopsis* bioherms: The first metazoan buildups following the end-Permian mass extinction. *Palaios* 22: 17–23.

Reeside, J.B. and Bassler, H. 1922. Stratigraphic sections in southwestern Utah and northwestern Arizona. *U.S. Geological Survey Professional Paper* 129-D: 53–77.

Reif, D.M. and Slatt, R.M. 1979. Red bed members of the Lower Triassic Moenkopi Formation, southern Nevada; sedimentology and paleogeography of a muddy tidal flat deposit. *Journal of Sedimentary Research* 49: 869–889.

Richter, R. 1937. Marken und Spuren aus allen Zeiten. I–II. *Senckenbergiana* 19: 150–163.

Rieth, A. 1932. Neue Funde spongeliomorpher Fucoiden aus den Jura Schwabens. *Geologische und Paläontologische Abhandlungen* 19: 257–294.

Savrda, C.E. and Bottjer, D.J. 1986. Trace-fossil model for reconstruction of paleo-oxygenation in bottom waters. *Geology* 14: 3–6.

Schlotheim, E.F. von 1820. *Die Petrefactenkunde auf ihrem jetzigem Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreichs der Vorwelt erläutert. Erste Abtheilung. Das Thierreich*. 437 pp. Beckersche Buchhandlung, Gotha.

Schindewolf, O.H. 1928: Studien aus dem Marburger Buntsandstein III–VI, *Senckenbergiana* 10: 16–54.

Schmidt, M. 1928. *Die Lebewelt unserer Trias*. 461 pp. Rau, Öhringen.

Schmidt, M. 1938. *Die Lebewelt unserer Trias; Nachtrag*. 144 pp. Rau, Öhringen.

Schubert, J.K. and Bottjer, D.J. 1995. Aftermath of the Permian–Triassic mass extinction event: Paleoecology of Lower Triassic carbonates in the western USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 116: 1–39.

Seilacher, A. 1967. Bathymetry of trace fossils. *Marine Geology* 5: 413–428.

Sepkoski, J.J. Jr. 1988. Alpha, beta or gamma: Where did all the diversity go. *Paleobiology* 14: 221–234.

Sokal, R. and Michener, C. 1958. A statistical method for evaluating systematic relationships. *University of Kansas Science Bulletin* 38: 1409–1438.

Stiller, F. 2001. Fossilvergesellschaftungen, Paläoökologie und paläosynökologische Entwicklung im Oberen Anisium (Mittlere Trias) von Qingyan, insbesondere Bangtoupo, Provinz Guizhou, Südwestchina. *Münstersche Forschungen zur Geologie und Paläontologie* 92: 1–523.

Szulc, J. 2007. Sponge-microbial stromatolites and coral-sponge reef recovery in the Triassic of the western Tethys domain. *In:* S.G. Lucas and J.A. Spielmann (eds.), The Global Triassic. *New Mexico Museum of Natural History and Science Bulletin* 41: 402.

Twitchett, R.J. and Wignall, P.B. 1996. Trace fossils and the aftermath of the Permo-Triassic mass extinction: evidence from northern Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology* 124: 137–151.

Wasmer, M., Hautmann, M., Hermann, E., Ware, D., Roohi, G., Rehman, K., Yassen, A., and Bucher, H. 2012. Olenekian (Early Triassic) bivalves from the Salt Range and Surghar Range, Pakistan. *Palaeontology* 55: 1043–1073.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon* 21: 213–251.

Whittaker, R.H. 1975. *Communities and ecosystems*. 385 pp. Macmillan; Collier Macmillan, New York.

Wignall, P.B. and Hallam, A. 1992. Anoxia as a cause of the Permian/Triassic mass extinction: facies evidence from northern Italy and the western United States. *Palaeogeography, Palaeoclimatology, Palaeoecology* 93: 21–46.

Wolda, H. 1981. Similarity indices, sample size and diversity. *Oecologia* 50: 296–302.

Zieten, C.H. von 1830. *Die Versteinerungen Württembergs*. 102 pp. Verlag & Lithographie des Werkes Unsere Zeit, Stuttgart.

Zonneveld, J.-P., Pemberton, S.G., Saunders, T.D.A., and Pickerill, R.K. 2002. Large, robust *Cruziana* from the Middle Triassic of northeastern British Columbia: Ethologic, biostratigraphic, and paleobiologic significance. *Palaios* 17: 435–448.

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Chapter 3

A new paleoecological look at the Dinwoody Formation (Lower Triassic, Western USA): intrinsic versus extrinsic controls one ecosystem recovery after the end-Permian mass extinction

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"He [Ludwig Wittgenstein] once greeted me with the question: "Why do people say that it was natural to think that the sun went round the earth rather than that the earth turned on its axis?" I replied: "I suppose, because it looked as if the sun went round the earth." "Well," he asked, "what would it have looked like if it had looked as if the earth turned on its axis?"

Elizabeth Anscombe, An Introduction to Wittgenstein's Tractatus (London 1959, p. 151)

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A NEW PALEOECOLOGICAL LOOK AT THE DINWOODY FORMATION (LOWER TRIASSIC, WESTERN USA): INTRINSIC VERSUS EXTRINSIC CONTROLS ON ECOSYSTEM RECOVERY AFTER THE END-PERMIAN MASS EXTINCTION

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ABSTRACT—The Dinwoody Formation of the western United States represents an important archive of Early Triassic ecosystems in the immediate aftermath of the end-Permian mass extinction. We present a systematic description and a quantitative paleoecological analysis of its benthic faunas in order to reconstruct benthic associations and to explore the temporal and spatial variations of diversity, ecological structure and taxonomic composition throughout the earliest Triassic of the western United States. A total of 15 bivalve species, two gastropod species, and two brachiopod species are recognized in the study area. The paleoecological analysis shows that the oldest Dinwoody communities are characterized by low diversity, low ecological complexity and high dominance of few species. We suggest that this low diversity most likely reflects the consequences of the mass extinction in the first place and not necessarily the persistence of environmental stress. Whereas this diversity pattern persists into younger strata of the Dinwoody Formation in outer shelf environments, an increase in richness, evenness and guild diversity occurred around the Griesbachian–Dienerian boundary in more shallow marine habitats. This incipient recovery towards the end of the Griesbachian is in accordance with observations from other regions and thus probably represents an interregional signal. In contrast to increasing richness within communities (alpha-diversity), beta-diversity remained low during the Griesbachian and Dienerian in the study area. This low beta-diversity reflects a wide environmental and geographical range of taxa during the earliest Triassic, indicating that the increase of within-habitat diversity has not yet led to significant competitive exclusion. We hypothesize that the well-known prevalence of generalized taxa in post-extinction faunas is primarily an effect of reduced competition that allows species to exist through the full range of their fundamental niches, rather than being caused by unusual and uniform environmental stress.

INTRODUCTION

THE END-PERMIAN mass extinction represents the most profound crisis in the history of metazoan life, with an estimated species loss of up to 96 percent in the marine realm (Raup, 1979). Starting with Hallam (1991), the ensuing recovery period received increasing attention. Studies of the post-extinction interval are important in order to understand how biota and ecosystems respond to massive environmental perturbations (Clapham and Payne, 2011), how rapidly ecosystems are able to recover and how evolutionary processes proceed in vacated ecospaces (e.g., Erwin, 2001; Brayard et al., 2009; Hofmann et al., 2013). Widely held assumptions on the Early Triassic recovery interval emphasize that ecosystem restoration was considerably delayed as a result of ongoing environmental stress (e.g., Wignall and Hallam, 1992) or of the intensity of species loss (Schubert and Bottjer, 1995). Recently, however, evidence emerged that the recovery was a more volatile process, with notable ecologic recovery taking place in benthic ecosystems on a much wider geographic scale (e.g., Krystyn et al., 2003; Beatty et al., 2008, Shigeta et al., 2009; Kaim et al., 2010; Hautmann et al., 2011; Hofmann et al., 2011) in the course of the Griesbachian and early Dienerian, i.e., considerably earlier than generally assumed. Paleoecological studies of the immediate post-extinction phase are, thus, of primary importance to resolve the questions if environmental stress was persistent in the early aftermath of the extinction and whether previously reported indications of early recovery were of local or of global significance. The Dinwoody Formation of the western U.S. records this critical time interval but with the exception of four quantitative samples presented by Schubert and Bottjer (1995), its faunal content has not yet been comprehensively studied with respect to paleoecology. Moreover, no modern taxonomic description of the fauna has been provided since the monograph of Ciriacks (1963) on Permian and Early Triassic bivalves from the western U.S. Here we present a quantitative paleoecological survey involving 40 sampled levels from nine sections spanning the full geographic and environmental range of the Dinwoody Formation. We aim to resolve recovery patterns of benthic ecosystems throughout the Griesbachian and lower Dienerian and across environmental gradients within the Dinwoody Formation and to integrate these results with recent advances in the understanding earliest recovery phase after the end-Permian mass extinction.

GEOLOGICAL AND STRATIGRAPHICAL SETTING

The Dinwoody Formation, which is recorded in Idaho, southwestern Montana, western Wyoming, and northern Utah (Fig. 1.2; Paull and Paull, 1994), represents a marine tongue deposited during a rapid Early Triassic transgression over a low-relief, terrestrial area that mainly exposed marine strata of Middle Permian age (Newell and Kummel, 1942; Paull and Paull, 1994). The Dinwoody Sea was an epicontinental embayment with connection to the Panthalassa Ocean to the west (Fig. 1.1). During Permian and Early Triassic times, the area remained tectonically quiescent (Paull and Paull, 1994). The maximum thickness of the Dinwoody Formation is about

750 meters in the depot center, located today in southeastern Idaho (Kummel, 1954). It pinches out towards the east in Wyoming and to the south in Utah (Fig. 1.2) (Newell and Kummel, 1942; Clark and Carr, 1984). General lithofacies patterns (e.g., Kummel, 1957; Clark and Carr, 1984; Paull and Paull, 1994) suggest that the Dinwoody Formation was deposited in a ramp-like configuration including inner shelf, outer shelf and deeper shelf environments.

The biostratigraphy of the Dinwoody Formation is not well constrained and of rather low resolution. Ammonites are very rare throughout the study area. Three conodont zones covering a time interval from the early Griesbachian to the Dienerian have been recognized in the Dinwoody Formation (Clark and Carr, 1984). Except for a general scheme as given in Clark and Carr (1984, fig. 1), a precise zonation with respect to lithostratigraphic relationships has never been worked out for the Dinwoody Formation. In terms of lithostratigraphy, the Dinwoody Formation is informally subdivided into three units in Wyoming (Newell and Kummel, 1942). These are the "Basal siltstone", the "*Lingula* zone", and the "*Claraia* zone". Kummel (1954) noted that this subdivision is not well developed in southeastern Idaho. During our field work, this zonation was difficult to recognize and practically of no value in localities other than in western Wyoming (Gros Ventre Canyon). Siltstones that would fit the descriptions of the "Basal siltstone" of Newell and Kummel (1942) are widespread throughout the Formation. Although there is a certain temporal dominance of *Lingula* in the lower part of the Formation, the occurrence of *Lingula* is generally related to local facies effects, which diminishes the stratigraphic utility of the "Lingula zone" of Newell and Kummel (1942). *Claraia mulleri* and *Claraia stachei* are closely related species which have been reported to co-occur in the same stratigraphic levels within the Dinwoody Formation (Newell and Kummel, 1942; Ciriacks, 1963). Although a precise biostratigraphic scheme has not been established, data from more offshore sections (e.g., Candelaria Formation, western Nevada), that facilitate a correlation with ammonoid data (Ware et al., 2011), suggest that these two species are abundant around the Griesbachian–Dienerian boundary interval.

We see some potential to establish a more reliable stratigraphic scheme by integrating sedimentological data (e.g., tracking relative sea level changes throughout the study area) with new conodont collections, but this is not within the scope of this study.

FIELD LOCALITIES AND METHODS

Fieldwork was conducted in August 2010 (by RH) in southwestern Montana and southeastern Idaho and in June 2011 (RH and MH) in western Wyoming, Montana, and northeastern Utah. Bed-by-bed logging and fossil sampling was performed at nine sections of the Dinwoody Formation. Detailed locality information can be found in Figure 1.2 and Table 1. Fossil collections were derived from discrete limestone and calcareous sandstone and siltstone beds, which were representatively sampled and mechanically decomposed for fossil extraction. Standard macro-invertebrate preparation techniques were performed to reveal morphologic details for taxonomic determination. Each collection was performed either until it yielded more than 100 specimens or until further sampling revealed no new finds of taxa. Occasionally, sampling was limited by poor exposures. Beds showing evidence of strong reworking, as for instance size-sorting, pronounced gradation or abundant abrasion of fossils, were not included in the quantitative analysis. Sampled intervals are suggested to represent autochthonous and para-autochthonous communities as bivalves are frequently observed in life position and are generally recorded as complete unabraded valves or molds of complete specimens. Identification of the sedimentological facies is based on field observations. Taxa recognized in this study include bivalves, gastropods, and brachiopods. The quantitative faunal list with absolute abundances is given in an Excel spread sheet available as an online Supplemental file.

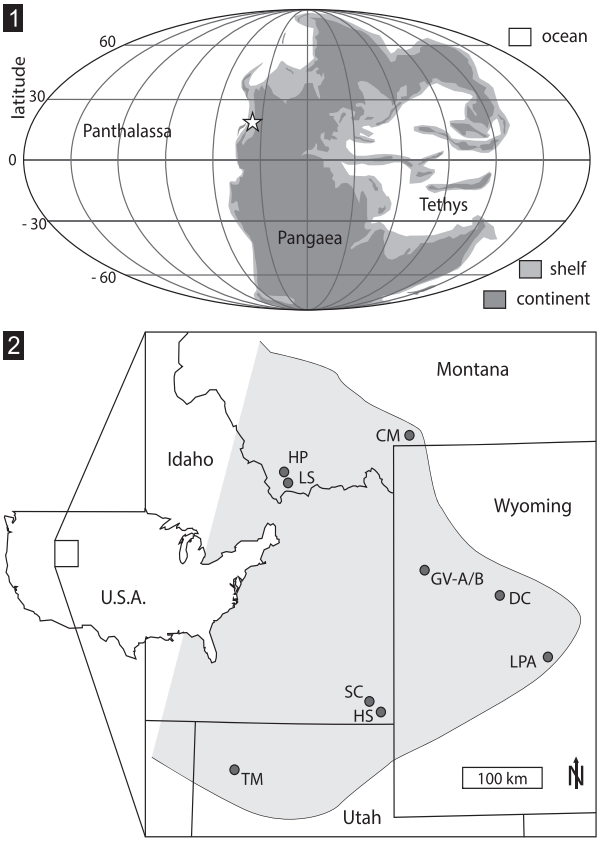

FIGURE *1—1*, global paleogeographic reconstruction for the Early Triassic after Blakey (2012); white star indicates the position of the Dinwoody Basin at the eastern Panthalassa margin; *2*, geographic positions of the measured sections and the extent of the Dinwoody Basin (grey shaded area) during the Griesbachian. After Paull and Paull (1994) referring to Maughan (1979).

Faunal abundance data were analysed with the software package PAST (Hammer et al., 2001). Cluster analysis followed the procedure applied in Hofmann et al. (2013), which also yielded the most reasonable groupings in the present data set, using the unweighted paired group method (UPGMA) as implanted in PAST in combination with the Morisita index of similarity (Morisita, 1959). The Q-mode cluster analysis groups samples into sets that are similar with respect to presence and abundance of taxa. This procedure is used to detect recurrent assemblages and to emphasize differences among distant groups. The dominance index D, as obtained from PAST (Hammer et al., 2001), was used as an inverse measure of ecological evenness.

Beta-diversity measures the degree of habitat partitioning along environmental gradients. A simple measure of beta-diversity is dividing the bulk number of taxa recorded in a set of adjacent communities (gamma diversity sensu Whittaker, 1972, 1975) by the average alpha-diversity of these communities

TABLE 1—Geographic information for the sections of the Dinwoody Formation visited during this study.

Code	Section	Geographic information	GPS coordinates (WGS 84)	Reference
LPA	Little Popo Agie Canyon	Wind River Range, Wyoming	N 42°40′27.90″, W 108°40′52.40″	Ciriacks (1963)
DC	Dinwoody Canyon	Wind River Range, Wyoming	N 43°21′31.70″, W 109°24′15.90″	Newell and Kummel (1942)
GV-A	Gros Ventre Canyon A	Gros Ventre Range, Wyoming	N 43°38′21.50″, W 110°34′27.90″	Newell and Kummel (1942)
GV-B	Gros Ventre Canyon B	Gros Ventre Range, Wyoming	N 43°38′10.30″, W 110°33′59.00″	Newell and Kummel (1942)
CM	Cinnabar Mountain	Gallatin Range, Montana	N 45°05′34.00″, W 110°47′28.50″	Ciriacks (1963)
LS	Little Sheep Creek	Tendoy Range, Montana	N 44°33′41.01″, W 112°42′43.41″	Scholten (1955)
HP	Hidden Pasture	Tendoy Range, Montana	N 44°40′38.00″, W 112°47′24.78″	Scholten (1955)
HS	Hot Springs Canyon	Bear Lake Area, Idaho	N 42°06′48.70″, W 111°15′16.90″	Kummel (1954)
SC	Sleight Canyon	Bear Lake Area, Idaho	N 42°14′03.29″, W 111°25′40.38″	Kummel (1954)
TM	Terrace Mountains	Box Elder County, Utah	N 41°27′51.10″, W 113°28′09.10″	Clark et al. (1977)

(Whittaker, 1975). However, because this approach is highly sensitive to the number of habitats in each set (everything else being equal, the larger set of habitats will have a higher beta-diversity), it is not very practical if it is aimed at comparing beta-diversity of different sets of communities at different stages of recovery. Another measure of beta-diversity is the coefficient of community or Jaccard Coefficient (Jaccard, 1901), as used by Sepkoski (1988). However, application of the Jaccard-coefficient for measuring beta-diversity requires an a priori recognition of neighboring habitats, which remains subjective in typical paleontological samples. These are generally scattered with respect to geography and time. In practice, paleocommunities occur variably within stratigraphic sections, and two communities recorded in strata, even in direct succession, may never represent two communities that lived adjacent to each other in the past.

In order to avoid these uncertainties, we introduce a new approach to calculate beta-diversity from paleontological data, based on mean minimum beta-diversity. In a first step, all samples that have been identified by the cluster analysis as belonging to the same association are pooled, resulting in a full list of species occurring in this association (this step corresponds to the standard reconstruction of species composition in paleocommunities; e.g., Aberhan 1992). Then, similarity coefficients between the different associations are calculated. We herein use the well-established Jaccard coefficient, although alternative similarity coefficients might be applicable as well. The resulting similarity matrix forms the basis for arranging associations according to the smallest differences in their taxonomic composition, which is used as an approximation of the former geographic arrangement. In a final step, the average values of beta-diversity between pairs of adjoining associations are calculated, giving a measure of habitat differentiation of the system as a whole.

The principal advantages of this procedure are 1) that it provides a standardized scheme of data treatment independent of subjective identification of neighbored habitats and 2) that beta-diversity values between different, stratigraphically separated sets of communities can be compared, regardless of the number of habitats recorded, because a higher number of habitats per se will not alter average beta-diversity between habitats, at least as long as the habitat gradient is more or less linear.

However, there are also problems with this method that have to be considered when interpreting mean minimum beta-diversity values. First, it should be noted that arranging associations according to minimum beta-diversity is just an approximation to former geographic relationships of these associations. However, this is also the case for any reconstruction based on sedimentary facies, and we think that the advantage of applying a standardized procedure outbalances this disadvantage in studies that primarily aim to compare beta-diversity between different sets of paleocommunities in time.

A more fundamental problem is that this method cannot measure progressing habitat contraction in a given set of paleoenvironments. If increasing competition leads to wedging new communities in-between the boundaries of existing paleocommunies, this will increase beta-diversity of the system as a whole but not necessarily average beta-diversiy between adjacent habitats, as measured by the mean minimum beta-diversity approach. This limits the application of the method to relatively early stages of recovery, when the number of competing species was relatively low and habitat contraction has not yet started. For the Early Triassic of the western U.S., it has recently been demonstrated that taxonomic differentiation between habitats was still low in the Spathian Virgin Formation (Hofmann et al., 2013), which represents a much more advanced recovery stage than the fauna of the Dinwoody Formation considered herein, according to overall diversity, number of guilds, and time elapsed since the mass extinction. In conclusion, the minimum beta-diversity approach is considered as the most appropriate method for comparing beta-diversity of the Dinwoody benthic faunas with those from the Virgin Formation, which is aimed herein.

SEDIMENTARY ENVIRONMENTS OF THE STUDIED SECTIONS

Gros Ventre Canyon (GV-A, GV-B).—Due to the spatial proximity, the two sections at the Gros Ventre Canyon are very similar in terms of their lithological succession (Fig. 2.1, 2.2). Where exposed, the lower interval is composed of laminated siltstones (Fig. 3.3) and claystones. The major part of the section is composed of laminated siltstones, silty sandstones, and sandstones that were most likely deposited under quiet water conditions. Some discrete, massive bioclastic limestone beds are intercalated. In the siliclastic intervals, ripple cross-lamination and trough cross bedding are frequently observed. Some massive sandstone beds show ball and pillow structures. All of these features indicate bedload deposition under the influence of waves and storms and, thus, argue for an inner shelf setting.

Wind River Range (LPA, DC).—The Dinwoody Formation in the Wind River Range of western Wyoming forms a mainly siliclastic wedge of shallow marine sediments thickening towards the northwest. The contact to underlying strata of Permian age is represented by a gap of unknown duration. The contact to the overlying continental red beds of the Chuggwater Formation seems conformable. At the Little Popo Agie Canyon locality sampled by us, the Dinwoody Formation (Fig. 2.3) is represented by a 5-m thick alternation of siltstone, sandstone, and marly limestone. Evidence for deposition in a shallow water environment is provided by the presence of abundant ripple cross-lamination and synaeresis cracks in the middle part of the section (Fig. 2.2). The section at Dinwoody Canyon is exclusively siliclastic and was found to be virtually unfossiliferous except for some poorly preserved internal molds and is therefore not included in the analysis.

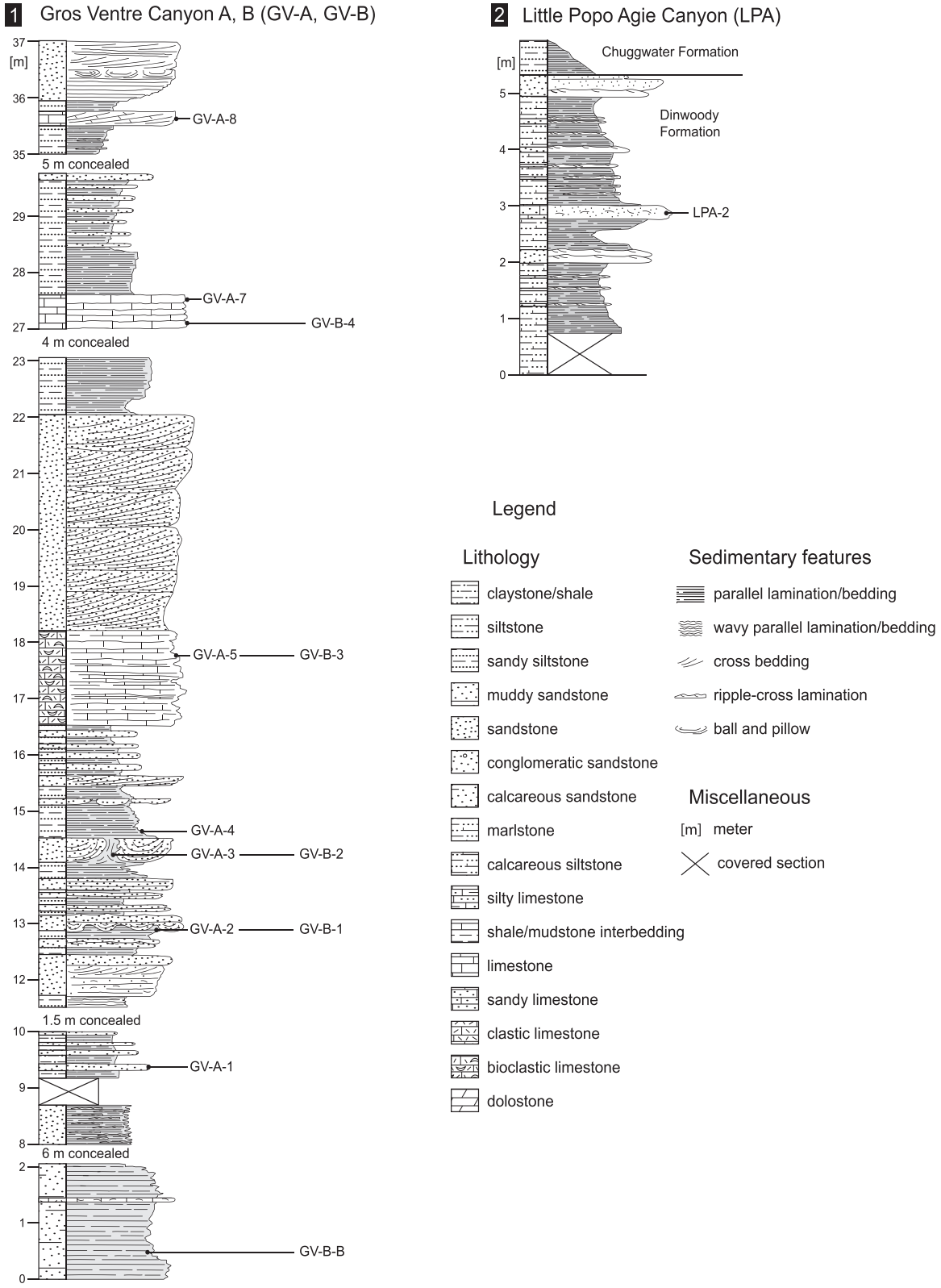

FIGURE 2—Sections of the Dinwoody Formation of western Wyoming and southern Montana. *1*, Gros Ventre Canyon; *2*, Little Popo Agie Canyon.

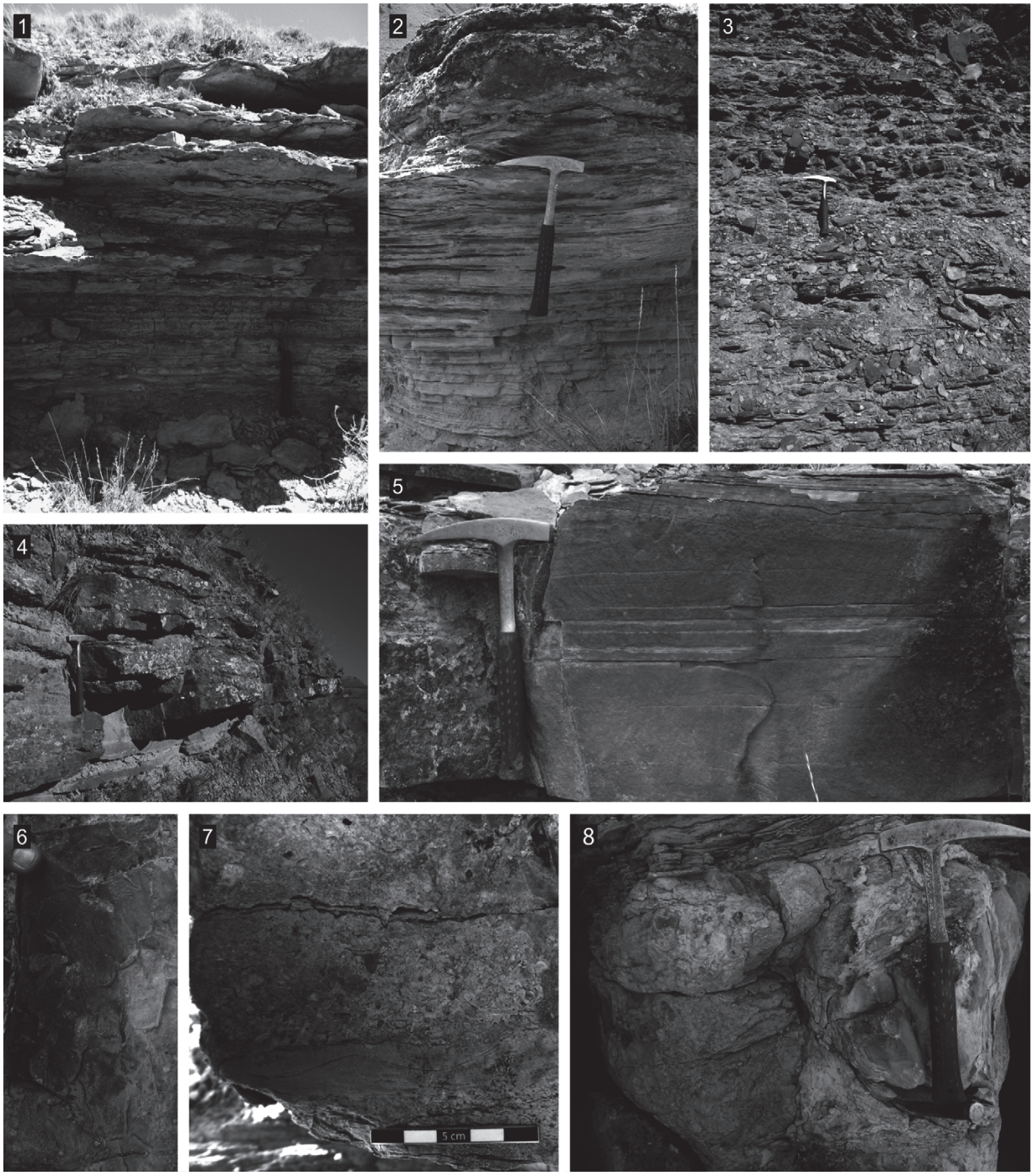

FIGURE 3—Sedimentary features and facies of the Dinwoody Formation of the Wind River Range, Gros Ventre Range, and the Tendoy Range. *1*, lower portion of the section LPA showing interbeddings of laminated calcareous siltstones and ripple cross-laminated sandstones of a lower shoreface facies; *2*, laminated siltstones topped by massive grainstones of the lower shoreface facies in section LS; *3*, rhythmic interbeddings of siltstones and fine-grained limestones of the lower part of section HP suggested to represent outer shelf deposits; *4*, massive grainstones of the inner shelf typical for the middle part of section HP; *5*, very fine-grained sandstones of the upper plane bed regime giving rise to cross-beds and waning of current energy, seen at section LS; *6*, synaeresis cracks diagnostic for salinity fluctuations, section LS; *7*, ripple cross-laminated calcareous sandstone giving rise to graded tempestitic bioclastic rudstone, top of section GV-A; *8*, ball and pillow-type deformation within sandstones typically recorded in the lower part of section GV-A. Hammer for scale=32 cm in height.

Cinnabar Mountain (CM).—At Cinnabar Mountain, 18 m of strata (Fig. 4.1) recognized as Dinwoody Formation (e.g., Ciriacks, 1963) are exposed between the strata of the Permian Shedhorn Sandstone Formation and red beds of presumably Triassic age. The contact to the underlying unit appears non-conformable. The section is dominated by laminated siltstones as well as bituminous and sandy packstones and grainstones. The comparably low thickness and the paleogeographic position of the

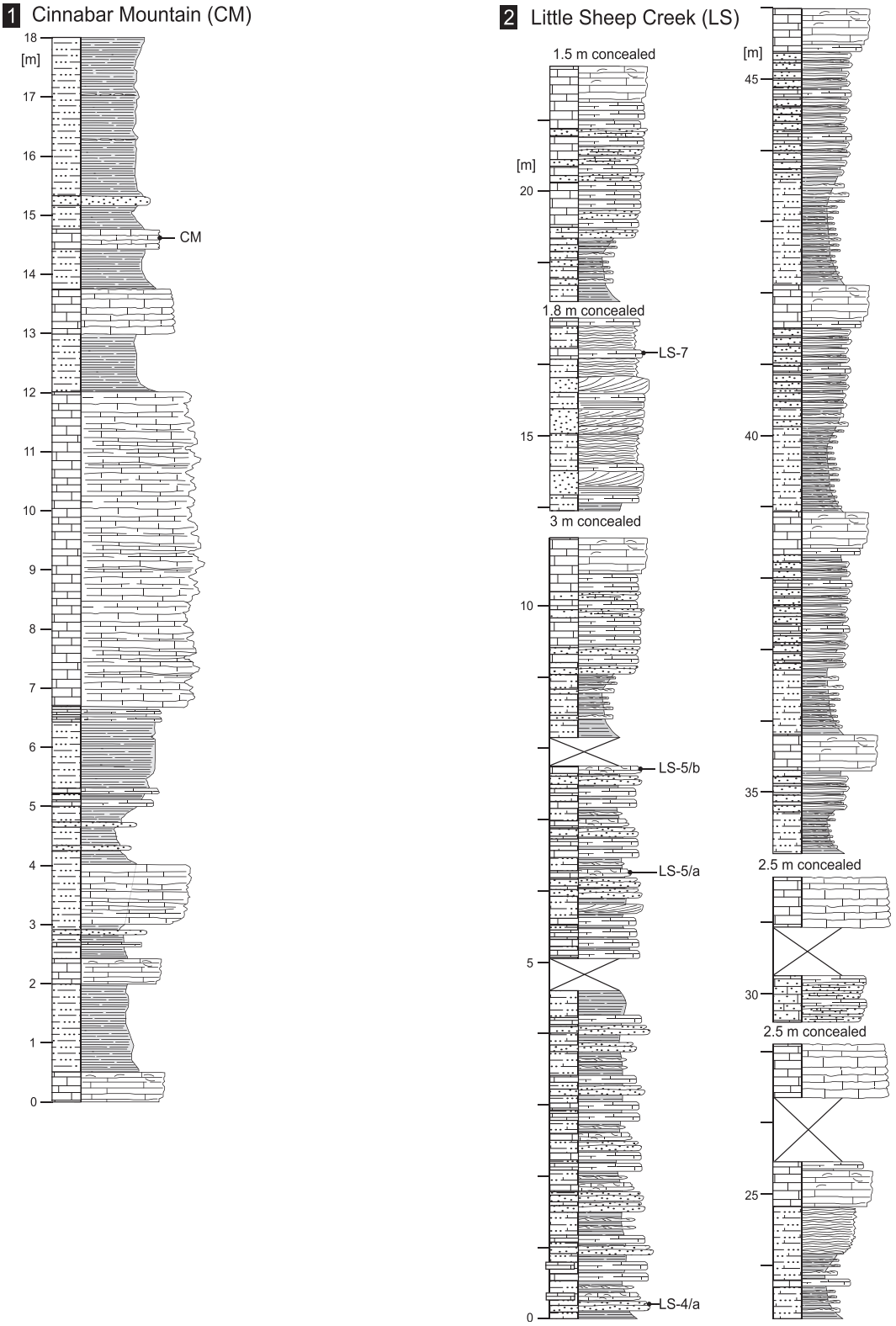

FIGURE 4—Sections of the Dinwoody Formation in southern Montana. *1*, Cinnabar Mountain Pasture; *2*, Little Sheep Creek.

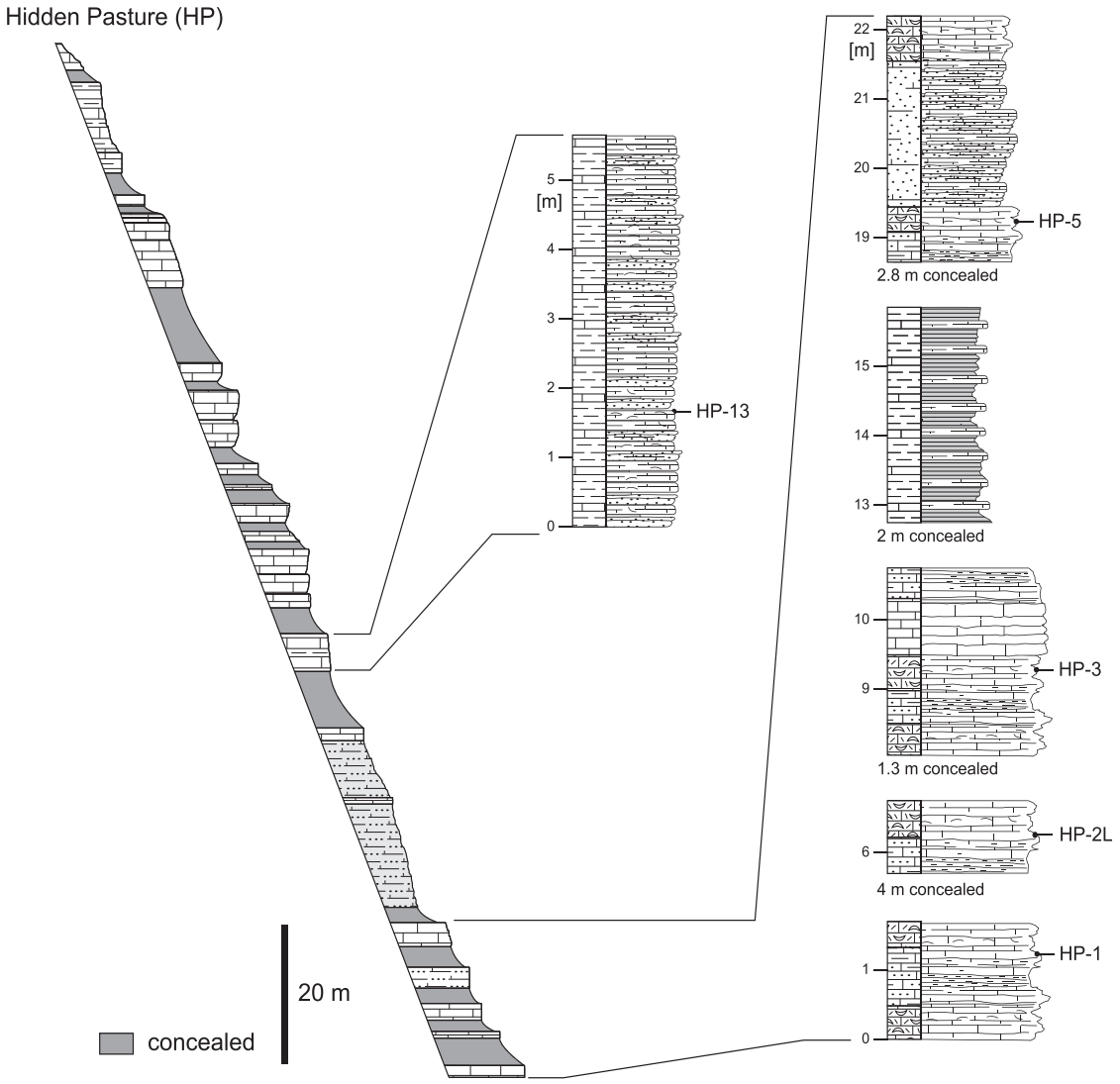

FIGURE 5—Section of the Dinwoody Formation at the Hidden Pasture locality of southern Montana.

section indicate that these strata were deposited in a rather proximal setting of the Dinwoody basin. The lack of criteria to recognize shallow and marginal marine deposition (e.g., cross bedding, ripple lamination, mud cracks) and the dominance of laminated siltstone as well as the high content of bitumina in the limestones suggests that this part of the basin was rather restricted with predominating quiet water conditions.

Tendoy Range (LS, HP).—In the Tendoy Range of southwestern Montana, the Dinwoody Formation attains a thickness of about 190 meters but pinches out towards the east and the north (Scholten et al., 1955). The Permian–Triassic transition has not been observed. The transition to the overlying red beds (Woodside Formation) appears to be gradual. In both the Little Sheep Creek (LS) (Fig. 4.2) and Hidden Pasture (HP) section (Fig. 5) visited during this study, the sedimentary record starts within Lower Triassic strata. These are composed of calcareous siltstones, fine-grained sandstones and limestones. Most siltstone intervals are poorly exposed. In the sandstone-dominated units, sedimentary structures including synaeresis cracks, wave and current ripple-lamination, trough cross-beds indicate shallow marine deposition in a wave-agitated environment. Most limestones are composed of massive bioclastic grainstone and rudstone and are intercalated within shallow marine sandstone beds. All sampled fossiliferous levels represent a shallow marine facies.

Bear Lake Area (HS, SC).—The section at Sleight Canyon (Fig. 6.1) is dominated by a monotonous succession of finely laminated siltstones. In the lower part, thin beds of very fine-grained sandstones are intercalated and levels with convolute bedding occur (Fig. 6.1). Some sets of siltstone beds show distinct lenticular lower boundaries (Fig. 7.5). Thin horizons with climbing ripples occur rarely within these beds. Despite the overall fine-grained nature of the deposits, these sedimentary signatures argue for fast deposition. Hence, this part of the section is interpreted to record sedimentary bypass of silt-size particles at the outer slope of the Dinwoody basin. The upper third of the section comprises slightly calcareous siltstones, which have a more massive appearance presumably due to increased bioturbation (Fig. 7.2) and wave activity as indicated by some ripple cross-laminated horizons. The section is topped by large-scale trough cross-bedded sandstones and capped by a distinct conglomerate bed.

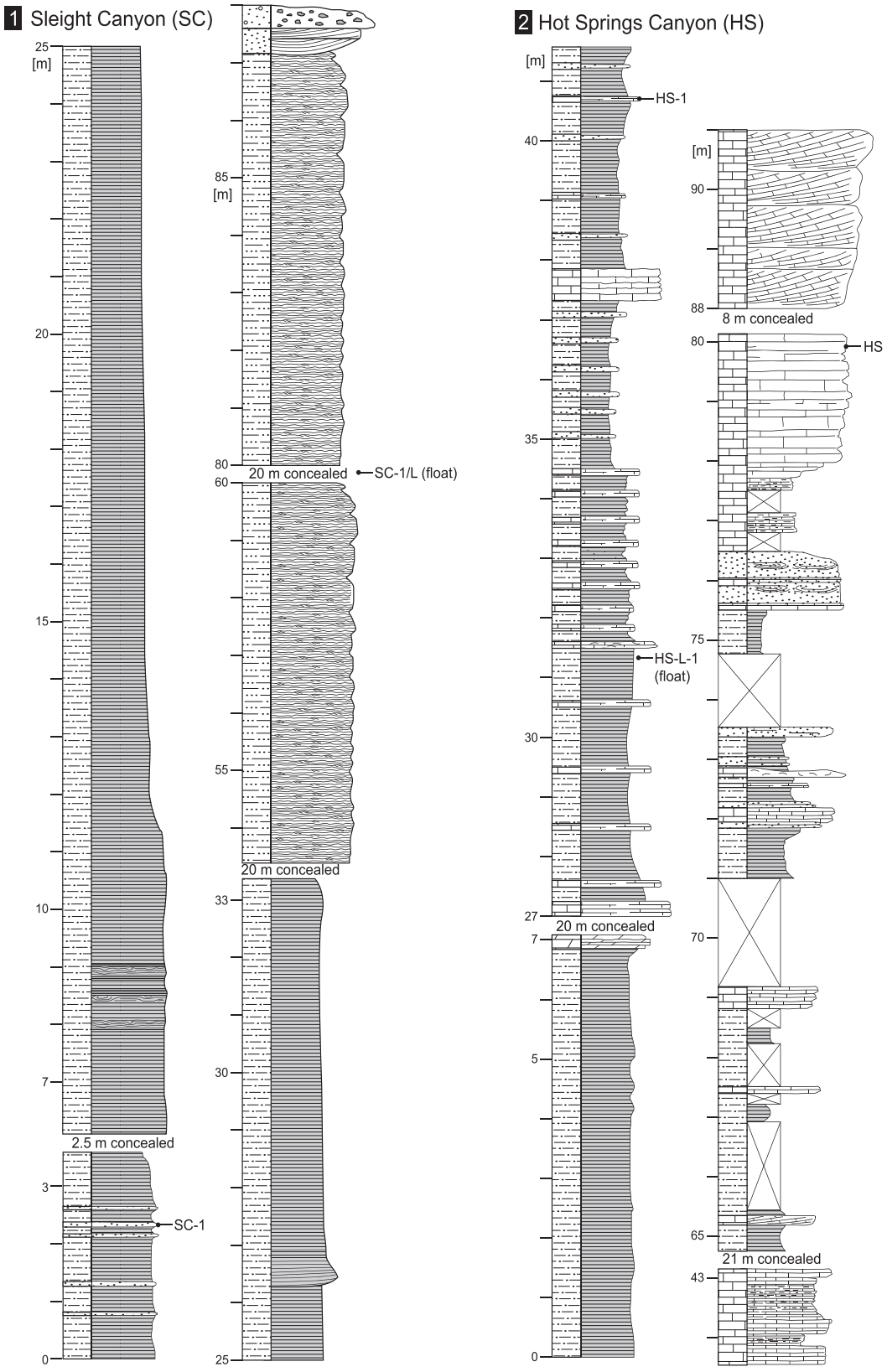

FIGURE 6—Sections of the Dinwoody Formation of southeastern Idaho. *1*, Sleight Canyon; *2*, Hot Springs Canyon.

FIGURE 7—Sedimentary features and facies of the Dinwoody Formation in the southwestern Idaho. *1*, laminated siltstone of the outer shelf, section SC; *2*, bioturbated siltstone intervals at the top of section SC; *3*, laminated shales and siltstones of the outer shelf/basinal facies, head of hammer pointing upsection, section HS; *4*, large scale trough cross-bedded sandstones interbedded with bioturbated siltstones indicating shallowing upward trend in section SC; *5*, incised wide-angle channels of siltstone in the middle part of section SC.

At Hot Springs Canyon (Fig. 6.2), the lower part is similarly developed with thin sandstone beds being more frequently intercalated. Discrete carbonate beds, mainly massive mudstone and floatstone, are intercalated towards the top of the section, which is capped by massive, indistinctly trough cross-bedded recrystallized limestone. The following interval is poorly exposed but reddish scree is indicative of the Woodside Formation. Both sections are largely unfossiliferous and all sampled levels are interpreted to have been deposited in outer shelf environments as suggested by the absence of sedimentary structures indicative of wave activity. This agrees well with paleogeographic reconstructions, which place the Bear Lake area within the offshore basin of the Dinwoody Basin (e.g., Paull and Paull, 1994).

Terrace Mountain (TM).—In this area, the Dinwoody is about 500 meter thick (Stifel, 1964). Because virtually the whole section is covered by vegetation or float, a reliable reconstruction of the sedimentary environment and logging of a continuous section at the Terrace Mountain locality was not possible. Rarely exposed massive limestone beds were sampled in an east–west transect perpendicular to the strike of the Terrace Mountain syncline. According to the description of Stifel (1964) and McCarthy and Miller (2002), the dominant lithotype is laminated siltstone. Based on the relatively large thickness and the overall dominance of fine-grained sediments, we infer that rocks of the Dinwoody Formation in this area were deposited in an outer shelf setting.

SYSTEMATIC PALEONTOLOGY

The taxonomy of the Dinwoody macroinvertebrate fauna is comparatively well known and identification of species is rather unproblematic using the studies of Girty (1927), Newell and Kummel (1942), Ciriacks (1963), and Newell and Boyd (1995) as a guideline for principle species identification. A most up-to-date monograph on a similar fauna from Far-Eastern Russia has been provided by Shigeta et al. (2009). All figured (Fig. 8) specimens are housed in the collection of the Paleontological Institute and Museum, Zurich University (abbreviation PIMUZ).

Class BIVALVIA Linnaeus, 1758
Infraclass AUTOLAMELLIBRANCHIATA Grobben, 1894
Subclass PTERIOMORPHA Beurlen, 1944
Order PTERIOIDA Newell, 1965
Suborder PTERIINA Newell, 1965
Superfamily AMBONYCHIOIDEA Miller, 1877
Family MYALINIDAE Frech, 1891
Genus MYALINELLA Newell, 1942

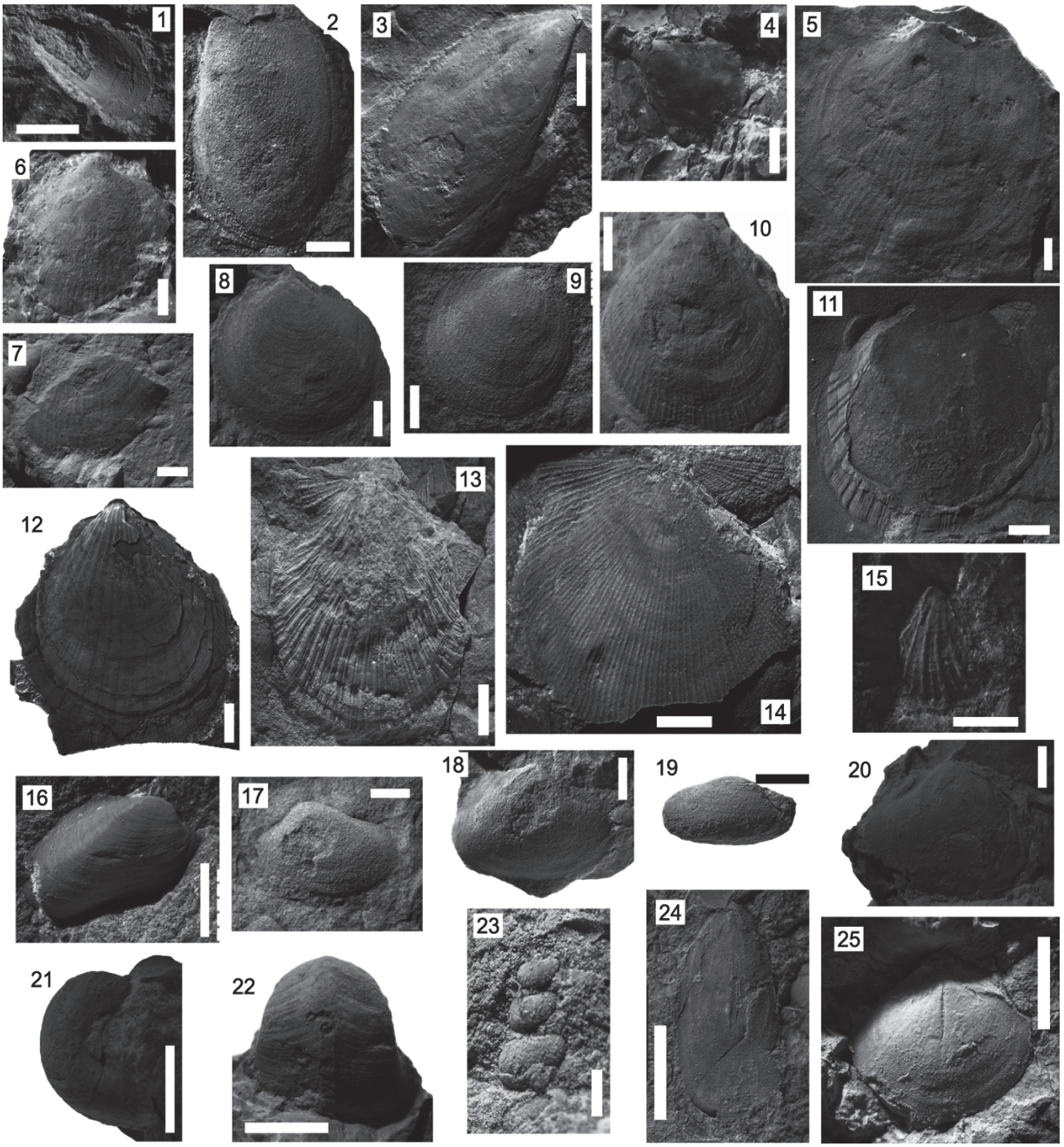

FIGURE 8—Body fossils of the Dinwoody Formation recognized in this study. *1*, *Myalinella postcarbonica*, right valve, HS, PIMUZ 30523; *2*, *Promyalina spathi*, left valve, GV-A-4, PIMUZ 30538; *3*, *Promyalina putiatinensis*, right valve, LPA-2, PIMUZ 30528; *4*, *Pteria*? *ussurica*, left valve, GV-A-8, PIMUZ 30540; *5*, *Claraia mulleri*, left valve, float at section GV-A, PIMUZ 30539; *6*, *Claraia mulleri*, left valve, GV-A-5, PIMUZ 30541; *7*, *Claraia* cf. *stachei*, left valve, LPA-A, PIMUZ 30529; *8*, *Claraia aurita*, left valve, CM, PIMUZ 30531; *9*, *Claraia aurita*, right valve, CM, PIMUZ 30532; *10*, *Leptochondria occidanea,* left valve, LPA-2, PIMUZ 30527; *11*, *Eumorphotis amplicostata*, left valve, HP-2L, PIMUZ 30537; *12*, *Eumorphotis amplicostata*, left valve, LS-5/b, PIMUZ 30536; *13*, *Eumorphotis multiformis*, left valve, LS-7, PIMUZ 30533; *14*, *Eumorphotis multiformis*, right valve, LS-7, PIMUZ 30534; *15*, *Eumorphotis* cf. *ericius*, left valve, LS-7, PIMUZ 30535; *16*, *Permophorus bregeri*, right valve, HS, PIMUZ 30524; *17*, *Unionites fassaensis*, left valve, GV-A-3, PIMUZ 30542; *18*, *Unionites fassaensis*, right valve, GV-B-1, PIMUZ 30543; *19*, *Unionites canalensis*, left valve, GV-B-2, PIMUZ 30544; *20*, *Neoschizodus laevigatus,* right valve, GV-A-5, PIMUZ 30545; *21*, *Dicellonema abrekensis* LPA-2, lateral view, PIMUZ 30526; *22*, *Dicellonema abrekensis,* , LPA-2, dorsal view, PIMUZ 30526; *23*, *Coelostylina* sp. A, HS, PIMUZ 30525; *24*, *Lingula borealis*, ventral valve, GV-B-B, PIMUZ 30546; *25*, *Periallus woodsidensis*, dorsal valve, TM-4, PIMUZ 30530. If not otherwise indicated, all scale bars=5 mm.

Myalinella postcarbonica (Girty, 1927)
Figure 8.1

1927 *Myalina postcarbonica* n. sp. Girty, p. 442, pl. 30, figs. 34, 35.
1942 *Mytilus*? *postcarbonica* (Girty); Newell and Kummel, p. 957.
1955 *Myalina* (*Myalinella*) cf. *meeki* Dunbar; Newell, p. 26, pl. 5, figs. 9, 10.
1963 *Mytilus*? *postcarbonica* (Girty); Ciriacks, p. 75, pl. 15, fig. 7.
2011 *Myalinella newelli* sp. nov.; Hautmann et al., p. 75, fig. 4.2–4.

Description.—Subequivalved, with left valve being slightly more inflated. Shell outline subtrigonal, slender and highly retrocrescent with round posteroventral margin. Anterior margin straight or almost so. Beaks subterminal, grading into distinct diagonal ridges. Surface of valves smooth except for faint commarginal growth lines. Internal features unknown.

Material.—Rarely recorded in HS, LPA-2, CM and GV-A-8. The description is based on a very well preserved left valve from LPA-2 (PIMUZ 30523).

Remarks.—Hautmann et al. (2011) pointed out that lower Triassic specimens from Greenland referred to as *Myalina* (*Myalinella*) cf. *meeki* by Newell (1955) are clearly distinguishable from Permian *Myalina meeki* by its more pronounced convexity of valves. Accordingly, Hautmann et al. (2011) introduced the new species *Myalinella newelli* for this lower Triassic material. The descriptions and figures provided by Girty (1927) reveal that the specimens from the lower Triassic of the western U.S. share the same diagnostic features with those given by Hautmann et al. (2011). Thus, we regard *M. newelli* a younger synonym of *M. postcarbonica*. *Myalina postcarbonica* is a cosmopolitan species being reported from the equatorial (Girty, 1927) and boreal (Newell, 1955) eastern Panthalassa margin as well as the eastern Tethys (Hautmann et al., 2011).

Myalinella postcarbonica is interpreted as a byssally attached, epifaunal suspension feeder resting orthothetically on the flat anterior-ventral margin (Stanley, 1972).

Genus Promyalina Kittl, 1904
Promyalina putiatinensis (Kiparisova, 1938)
Figure 8.3

1899 *Myalina vetusta* (Benecke) Bittner, 1899, 17, pl. 4, figs. 17–19.
1938 *Myalina putiatinensis*. Kiparisova; 261, pl. 6, figs. 10–12.
1942 *Myalina putiatensis* Kiparisova [sic]; Newell and Kummel, p. 957, pl. 3, figs. 9, 10.
1963 *Promyalina putiatensis* (Kiparisova) [sic]; Ciriacks, p. 75, pl. 16, figs. 1–5.
2009 *Promyalina putiatinensis* (Kiparisova); Kumagae and Nakazawa, p. 157, fig. 144.4, 144.5.

Description.—Relatively large shell up to 6 cm in height, subequivalved with right valve being less inflated, retrocrescent, higher than long, mytiliform, weakly inflated. Angle between slightly convex anterior margin and straight dorsal margin considerably less than 90°. Arcuate ventral margin, posterior margin rounded. Umbo terminal at anterior end. Surface smooth except for irregular growth lines.

Material.—Recorded in GV-A-3, 13 in LPA-2. The description is based on a well preserved right valve from sample LPA-2 (PIMUZ 30528).

Remarks.—*Promyalina putiatinensis* is a common element in Early Triassic faunas of the Panthalassic margin (Bittner, 1899; Newell and Kummel, 1942; Hautmann et al., 2013). It is distinguished from other species of the genus by its slender shape.

The lack of an anterior lobe, the more acline growth form suggests that *Promyalina putiatinensis* was a bysally attached, epifaunal filter feeder resting on its less inflated right valve (Stanley, 1972).

Promyalina spathi (Newell and Kummel, 1942)
Figure 8.2

1941 *Myalina* aff. *schamarae* (Bittner); Newell and Kummel, 1941, pl. 1, fig. 2.
1942 *Myalina spathi* n. sp. Newell and Kummel; p. 956, pl. 3, fig. 11.
1963 *Promyalina spathi* (Newell and Kummel); Ciriacks, p. 76, pl. 16, fig. 6.

Description.—Shell equivalved, retrocrescent, considerably higher than long, subquadrate in outline, weakly inflated. Angle between straight anterior margin and straight dorsal margin 90° or almost so. Posterior-ventral margin rounded. Umbo terminal at anterior end. Surface smooth except for irregular growth lines.

Material.—Rarely recorded with single valves in GV-A/B. More frequently observed in LS, LPA, and CM. The description is chiefly based on the specimen (PIMUZ 30538).

Remarks.—*Promyalina spathi* may be easily confused with other Early Triassic species of this genus (see Newell and Kummel, 1942; Newell, 1955). *Promyalina putiatinensis* is usually much more slender and is distinctly retrocrescent (Hautmann et al., 2013), and *P. schamarae* is characterized by a convex anterior margin (Kumagae and Nakazawa, 2009). *Promyalina groenlandica* differs in having beaks that project beyond the anterior margin (Newell, 1955). This feature is typical of *Promysidiella* (Waller, 2005), which suggests that *P. groenlandica* belongs to this genus, or that *Promysidiella* might had derived from *Promyalina. Promyalina spathi* is exclusively reported from the Early Triassic of the western U.S. (Newell and Kummel, 1942; Ciriacks, 1963).

Ecology is same as for *Promyalina putiatinensis*.

Superfamily Pterioidea Gray, 1847
Family Pteriidae Gray, 1847
Genus Pteria Scopoli, 1777
Pteria? cf. ussurica (Kiparisova, 1938)
Figure 8.4

cf.1899 *Gervilleia* cfr. *exporrecta* Lepsius; Bittner, p. 15, pl. 3, figs. 1–6.
1938 *Gervillia usssurica* sp. nov.; Kiparisova, p. 241, pl. 6, figs. 5, 6.
1942 *Gervillia usssurica* Kiparisova; Newell and Kummel, p. 959.
1963 *Gervilleia* cf. *ussurica* Kiparisova; Ciriacks, p. 76, pl. 16, fig. 10.
cf.2009 *Pteria ussurica* (Kiparisova); Kumagae and Nakazawa, p. 158, fig. 144.6–144.8.

Description.—Shell small, inequilateral and oblique. Inequivalved, left valve moderately inflated, right valve feebly inflated. Umbo slightly projecting above straight hingeline. Angle between hinge line and line of maximum inflation about 35° to 45°. Anterior wing very small and rounded. Posterior wing flat. Shell externally smooth. Internal features not observed.

Material.—Very common in sections GV-A, GV-B, LPA. Rarely recorded in lower part of HP and LS. Preserved as internal molds only. The description is based on numerous comparably well preserved right and left valves in sample GV-A-8 (PIMUZ 30540).

Remarks.—Similar material that was described from the same

unit has usually been referred to as "*Gervilleia*" *ussurica* (see synonymy). Kiparisova and Krishtofovich (1954) observed a single ligament groove in the type material of *Gervilleia ussurica* and, thus, emended it to *Avicula* (=*Pteria*), which has been adopted by Kumagae and Nakazawa (2009). However, in discussing distinction between Early Triassic *Pteria* and *Bakevellia* species, Hautmann et al. (2011) noted that a single ligament groove is also present in early ontogenetic stages of *Pteria*, whereas multiple resilifers occasionally occur as variations of the alivincular ligament system (e.g., Hautmann, 2004). Although this complicates the distinction of both genera, we provisionally follow the currently established scheme (cf. Kumagae and Nakazawa, 2009).

Recent *Pteria* species live epibyssally (Stanley, 1972). However, as suggested by Stanley (1972), this habit may have evolved from an endobyssate ancestral stage. Because the morphology of *Pteria ussurica* is comparable to Mesozoic *Bakevellia* species that have been interpreted as endobyssate (semi-infaunal) filter feeders (Muster, 1995; Aberhan and Muster, 1997), we assume the same habit for *P. ussurica*.

Superfamily Pterinopectinoidea Newell, 1938
Family Pterinopectinidae Newell, 1938
Genus Claraia Bittner, 1901
Claraia mulleri Newell and Kummel, 1942
Figure 8.5, 8.6

1942 *Claraia mulleri* n. sp.; Newell and Kummel, p. 956, pl. 3, figs. 3, 4.
1963 *Claraia mulleri* Newell and Kummel; Ciriacks, p. 79, pl. 15, fig. 8.

Description.—Orbicular to oval in outline, slightly longer than high. Left valve feebly convex with central, orthogyrate umbo projecting above dorsal margin. Anterior auricle absent on left valve as indicated by oblique anterior-dorsal margin. Posterior-dorsal margin straight with broad posterior auricle. Left valve covered with about 30 faint radial ribs. Right valve and internal features not observed.

Material.—The description is based on five left valves from GV-A-5 (e.g., PIMUZ 30541), one specimen from float at section GV-A (PIMUZ 30539).

Remarks.—*Claraia stachei* and *C. mulleri* are characterized by distinct radial ribs whereas commarginal folds and ribs, otherwise typical for the genus, are less pronounced or absent. Bittner (1901) erected *C. stachei* based on specimens from the Lower Triassic of northern Italy, which however were not figured (Ware et al., 2011). Spath (1930) assigned material from the Lower Triassic of Greenland to this species based on the description of Bittner (1901). Subsequent authors largely used the specimens described and figured by Spath (1930) as reference for identification of this species although it is still unclear whether the material of Spath (1930) corresponds to that of Bittner (1901). *Claraia mulleri* has been introduced by Newell and Kummel (1942). However, their descriptions and figures of both species *C. mulleri* and *C. stachei* reveals no distinct differences apart from a more developed, subquadrate posterior auricle in left valves in *C. mulleri*. The same feature can be observed in the figures provided by Ciriacks (1963), who reported both species from the "*Claraia* Zone" of the Dinwoody Formation. The identification of this species in our material is based on the general outline, and the shape of the posterior auricle of the left valve. Furthermore, Newell and Kummel (1942) and Ciriacks (1963) observed *C. mulleri* exclusively in the Gros Ventre Caynon, which agrees with our observation. However, *C. mulleri* has recently also been desribed from the lowermost Dienerian of the Candelaria Hills (Nevada; Ware et al., 2011)

The presence of a byssal sinus and a flat right valve suggest that *Claraia mulleri* was a bysally attached, epifaunal filter feeder.

Claraia cf. stachei Bittner, 1901
Figure 8.7

cf.1901 *Pseudomonotis* (*Claraia*) *stachei* n. sp.; Bittner, p. 587.
1930 *Claraia stachei* Bittner; Spath, p. 46, fig. 5.
1942 *Claraia stachei* Bittner; Newell and Kummel, p. 955, pl. 3, figs. 5–8.
1963 *Claraia stachei* Bittner; Ciriacks, 1963, p. 79, pl. 15, figs. 1–3.

Description.—Feebly inflated left valve covered with fine radial ribs.

Material.—Two left valves from LPA-2 are the only recorded specimens (PIMUZ 30529).

Remarks.—The differences between the two similar species *C. stachei* and *C. mulleri* is outlined in the remarks on *C. mulleri*. Although species distinction cannot be made on the material recovered from the section LPA due to incomplete shell preservation, we are inclined to refer these specimens provisionally to *C. stachei* because this species is much more widerspread whereas in the Dinwoody Formation *C. mulleri* seems to be confined to a local occurrence in the Gros Ventre Canyon area (Newell and Kummel, 1942; Ciriacks, 1963). *Claraia stachei* is widely reported from the Panthalassic margin (e.g., Ciriacks, 1963; Spath, 1930; Shigeta et al., 2009) and it is confined to rocks of upper Griesbachian to lower Dienerian age (Shigeta et al., 2009; Ware et al., 2011).

Ecology is same as for *Claraia mulleri*.

Claraia aurita (Hauer, 1850)
Figure 8.8, 8.9

1850 *Posidonomya aurita* Hauer, p. 12, pl. 3, fig. 5.
1901 *Pseudomonotis aurita* Hauer; Bittner, p. 587, pl. 14, figs. 10–12.
1977 *Claraia aurita* Hauer; Nakazawa, p. 291, pl. 3, fig. 12 (cum synonymis).

Description.—Shell suborbicular in outline, slightly retrocrescent, inequivalved. Left valve moderately convex for the genus, umbo nearly orthogyrate, projecting above dorsal margin. Anterior auricle absent, posterior auricle obtuse, with prosocline incremental lines. Right valve feebly inflated, umbo not projecting above straight hinge line. Right anterior auricle small, shape of byssal notch not observed. Both valves covered with fine, regular commarginal striae.

Material.—The description is based on three left valves (e.g., PIMUZ 30531), four right valves (e.g., PIMUZ 30532), and three incomplete valves from CM.

Remarks.—*Claraia aurita* is a cosmopolitan species but it is virtually unknown from eastern Panthalassa. The only report of this species from the western U.S. comes from the Candelaria Formation of western Nevada (Muller and Furgison, 1939). However, these authors did not figure any material, and this occurrence has never been confirmed by other studies. The record of this species in the Dinwoody Formation represents the first well-documented report from the eastern Panthalassa margin. In the Tethys, this species is considered diagnostic for strata overlying the *C. clarai* zone (e.g., Broglio-Loriga et al., 1990) and, thus, it is suggested to represent an exclusive Dienerian species. However, new collections from the Werfen Formation of northern Italy, which are currently under investigation by the authors, reveal that typical Griesbachian species of the "*Claraia aurita* group" (Nakazawa, 1977) such as *C. wangi, C. griesbachi, C. orbicularis* and *C. concentrica* are not clearly distinguishable

from *C. aurita,* which would question the stratigraphic significance of this species. However, given the limited material observed in the Dinwoody Formation, it is beyond the scope of this study to clarify synonymies among these very similar forms.

Ecology is same as for *Claraia mulleri*.

Suborder Pectinina Waller, 1978
Superfamily Aviculopectinoidea Meek and Hayden, 1864
Family Asoellidae Begg and Campbell, 1985
Genus Leptochondria Bittner, 1891

Remarks.—We follow Hautmann et al. (2013) in regarding Leptochondriidae Newell and Boyd, 1995 as a younger synonym of Asoellidae.

Leptochondria occidanea (Meek, 1877)
Figure 8.10

1877 *Aviculopecten occidaneus*; Meek, p. 96, pl. 12, fig. 13–13b.
1927 *Monotis superstricta* (White) var. *parksi* n. var.; Girty, p. 441, pl. 30, figs. 20, 21.
1995 *Leptochondria occidaneus* (Meek) [sic]; Newell and Boyd, p. 70, fig. 51.3–51.9.

Description.—Equilateral, orbicular shell, slightly higher than long. Left valve convex with orthogyrate umbo slightly projecting above straight dorsal margin. Anterior auricle well demarcated from disc with shallow auricular sinus. Posterior auricle not preserved. Left valve covered with about 40 simple evenly spaced radial ribs and very fine commarginal growth lines. Right valve and internal features not observed.

Material.—Several specimens with variable preservation occur in the samples of section TM and LS-4/a. The description is based on one well preserved left valve from the sample LPA-2 (PIMUZ 30527).

Remarks.—*Leptochondria* is notorious for the absence of right valves (e.g., Wasmer et al., 2012; Hautmann et al., 2013), which is most likely related to their weak calcification (Newell and Boyd, 1995). Thus, species identification largely relies on sculpture as well as auricle and disc morphology (Hautmann et al., 2013) of the left valve. The specimens from the Dinwoody Formation agree well with the features of *L. occidanea* as figured in Newell and Boyd (1995) including a relatively pronounced anterior auricular sinus, a well-demarcated disc and second order ribs inserted by intercalation. However, we note that the ribs are considerably finer and more numerous than in the specimens figured by Newell and Boyd (1995). This species has been widely reported from the younger (Smithian and Spathian) Thaynes Formation of the western U.S. (Girty, 1927; Newell and Boyd, 1995).

Right valves of this species (see Newell and Boyd, 1995; Hautmann et al., 2013) are flat and possess a deep byssal notch, which suggests that *Leptochondria occidanea* was a bysally attached, epifaunal filter feeder.

Family Heteropectinidae Beurlen, 1954
Genus Eumorphotis Bittner, 1901a
Eumorphotis amplicostata Ciriacks, 1963
Figure 8.11, 8.12

1963 *Eumorphotis amplicostata* new species; Ciriacks, p. 77, pl. 15 figs. 10–12.

Description.—Left valve suborbicular, almost equilateral to slightly retrocrescent, slightly higher than long, moderatetly inflated. Umbo orthogyrate and slightly projecting above straight hingeline, slightly in front of midpoint of dorsal margin. Anterior auricle with shallow auricular sinus and well demarcated from disc. Posterior auricle triangular with smooth transition to the umbonal flank. Radial ornamentation with paired, prominent grooves bordering smooth, flat to faintly rounded ridges. Up to six very faint ribs intercalated. Faint commarginal growth lines present. Right valves and internal features unknown.

Material.—This species occurs in the sections HP and LS. The description is based on five, well-preserved left valves from sample LS-5/b (e.g., PIMUZ 30537, PIMUZ 30536).

Remarks.—This species is readily recognized by means of its characteristic shell ornamentation. A probably closely related species showing a similar radial sculpture with broad rounded ridges is *E. duronicus* from the Werfen Formation of northern Italy (Wittenburg, 1908; section "Campitello" presumably exposing the Seis Member, sensu Broglio-Loriga et al., 1983). However, *E. duronicus* is significantly higher than long and spacing between the ridges is much narrower. *E. amplicostata* is known from the Dinwoody Formation only (Ciriacks, 1963).

The auricular sinus seen in the left valves at hand suggest that *Eumorphotis amplicostata* was a bysally attached, epifaunal filter feeder.

Eumorphotis multiformis (Bittner, 1899)
Figure 8.13, 8.14

1899 *Pseudomonotis multiformis*; Bittner, p. 10, p1. 2, figs. 15–22.
1942 *Eumorphotis multiformis* (Bittner); Newell and Kummel, p. 957, p1. 2, figs. 10, 11.
1963 *Eumorphotis multiformis* (Bittner); Ciriacks, p. 77, pl. 15, figs. 13, 15.
1963 *Eumorphotis multiformis regularaecosta* Kiparisova; Ciriacks, 1963, p. 77, pl. 15, fig. 14.
2009 *Eumorphotis multiformis* (Bittner); Kumagae and Nakazawa, p. 162, fig. 144.17 (cum synonymis).

Description.—Left valve weakly to moderately inflated, almost equilateral, infracrescent. Umbo orthogyrate, slightly projecting above straight hinge line and placed centrally. Anterior auricle well demarcated from disc, with shallow auricular sinus. Posterior auricle not observed. Left valve covered with three orders of radial ribs being irregularly intercalated. Some ribs weakly squamose. Right valve flat or almost so. Anterior auricle wing-like, with narrow byssal notch. Posterior auricle small and obtuse. Radial ornamentation with two orders of ribs, with the second order being irregularly intercalated. Reticular ornamentation well developed on anterior auricle.

Material.—Very common in HP and LS. The description is based on several left valves and one right valves from sample LS-7 (e.g., PIMUZ 30533, PIMUZ 30534).

Remarks.—*Eumorphotis multiformis* is characterized by multiple orders of intercalated, mostly smooth radial ribs. It includes forms that are highly variable with regard to the order and number of radial ribs allowing no clear distinction of discrete morphotypes. Earlier workers introduced a number of varieties or subspecies of *E. multiformis* to render morphologic differences (for overview see Broglio Loriga and Mirabella, 1986). We follow the more recent taxonomic practice (see Kumagae and Nakazawa, 2009) and consider the various subspecies of *E. multiformis* as synonyms of a highly variable species. *Eumorphotis multiformis* has a cosmopolitan distribution and is reported from the Griesbachian (Ciriacks, 1963), Dienerian (Broglio Loriga and Mirabella, 1986) and the Spathian (Hautmann et al., 2013).

Ecology is same as for *Eumorphotis amplicostata*.

Eumorphotis cf. ericius Hautmann et al., 2013
Figure 8.15

?1908 *Pseudomonotis beneckei* Bittner; Wittenburg, 1908, p. 29, pl. 4, fig. 1.

cf.2013 *Eumorphotis ericius*; Hautmann et al., pl. 2, figs. 8–12.

Description.—Valve small, retrocrescent, auricles not observed. Two distinct orders of squamose ribs. A third set of radial ribs is faintly developed.

Material.—Thirty-one left valves from LS-7 (e.g., PIMUZ 30535).

Remarks.—In terms of ornamentation, the material is indistinguishable from *E. ericius*, which has been described from the younger Virgin Formation (late Early Spathian of the western U.S.). The small size of the specimens observed in the Dinwoody Formation could explain that it has been overlooked in previous studies (see Hautmann and Nützel, 2005).

Ecology is same as for *Eumorphotis amplicostata*.

Subclass Heteroconchia Hertwig, 1895
Superorder Palaeoheterodonta Newell, 1965
Order Modiomorphoida Newell, 1969 *in* Cox et al., 1969
Superfamily Modiomorphoidea Miller, 1877
Family Kalenteridae Marwick, 1953
Genus Permophorus Chavan, 1954
Permophorus bregeri (Girty, 1927)
Figure 8.16

1927 *Pleurophorus bregeri* n. sp.; Girty, p. 445, pl. 30, figs. 40, 41.
1927 *Pleurophorus similis* n. sp.; Girty, p. 446, p1. 30, figs. 38, 39.
1927 *Pleurophorus rotundus* n. sp.; Girty, p. 446, pl. 30, figs. 42, 43.
1942 *Pleurophorus*? *bregeri* Girty; Newell and Kummel, p. 957, p1. 2, fig. 12.
1963 *Permophorus*? *bregeri* (Girty); Ciriacks, p. 83, pl. 16, figs. 8, 9.

Description.—Valves equivalved, trapezoidal to subrectangular in outline, posteriorly elongated, moderately to strongly inflated. Umbo strongly prosogyrate with beak located at anterior 20 percent or less of dorsal margin. Anteriordorsal margin rounded, lunule small. Posteriordorsal margin straight, escutcheon narrow. Ventral margin straight to slightly arcuate. Shell covered with closely spaced commarginal growth lines. Umbonal ridge more or less pronounced tending to smooth out towards posterior part of the shell. Internal features not observed.

Material.—Very common in sample HS. Description based on well preserved material including three left valves and four right valves (e.g., PIMUZ 30524).

Remarks.—Newell and Kummel (1942) already speculated that the three species of "*Pleurophorus*" (*P. similis, P. bergeri*, and *P. rotundus*) described by Girty (1927) belong to the same species. Although the type material has not been restudied, Ciriacks (1963) placed them all in synonymy based on the description of Girty (1927), who noted that the general morphological characters tend to be highly intergradational and, thus, making species distinction difficult. In the Dinwoody Formation, *Permophorus* seems to be restricted to strata from southeastern Idaho (Girty, 1927; Newell and Kummel, 1942; Ciriacks, 1963). In Mansfield (1927), lithologies that were later clearly recognized as the Dinwoody Formation (e.g., Newell and Kummel, 1942) were included in the Woodside Shale. Thus, all fossil occurrences ascribed to the Woodside Shale in Girty (1927) most likely refer to strata of the Dinwoody Formation. *Permophorus triassicus* (Newell and Boyd, 1999) from the upper Thaynes Formation (Spathian) differs from *P. bregeri* in lacking a well developed umbonal ridge and having a more arcuate dorsal margin.

Permophorus bregeri was a shallow infaunal suspension feeder (Stanley, 1972).

Superfamily Anthracosioidea Amalitsky, 1892
Family Anthracosiidae Amalitsky, 1892
Genus Unionites Wissmann, 1841 *in* Münster, 1841

Remarks.—We follow the revision of Geyer et al. (2005) that indicates assignment of *Unionites* to Anthracosiidae.

Different Early Triassic species have been assigned to *Unionites* on the basis of their general shape, but in none of these have internal shell characters or hinge dentition been described. Although we follow this convention, it is noted that some uncertainty remains until internal structures of these species become known.

Unionites canalensis (Catullo, 1846)
Figure 8.19

1848 *Tellina canalensis*; Catullo, p. 56, pl. 4, fig. 4.
1859 *Tellina* (*Myacites*) *canalensis* Catullo; Schauroth, p. 327, pl. 2, fig. 17.
1923 *Anodontophora canalensis* (Catullo); Diener, p. 230 (cum synonymis).
1963 *Unionites canalensis* (Catullo); Ciriacks, p. 81, pl. 16, figs. 11, 12.
2009 *Unionites canalensis* (Catullo); Kumagae and Nakazawa, p. 166, fig. 145.1–145.4 (cum synonymis).

Description.—Equivalved, outline elongate subelliptical. Nearly straight ventral margin. Umbones prosogyrate and projecting above dorsal margin. Beaks broad, located approximately in the mid of dorsal margin. Ventral margin round. Posterior margin blunt.

Material.—Recorded in samples HP-1, LS-5/a, LS-5/b, LS-4/a, GV-A-3, GV-A-4, GV-A-5, and GV-B-2. Preserved as internal and external molds. The description is based on some better preserved external molds of sample GV-B-2 (e.g., PIMUZ30544).

Remarks.—*Unionites canalensis* is a widely reported species from lower Triassic rocks and distinguished from the similar *U. fassaensis* by its more elongated outline and more pronounced umbonal ridge (Kumagae and Nakazawa, 2009). Ciriacks (1963) noted that umbones in *U. canalensis* are placed in a median position, which applies to our material as well. However, Hautmann et al. (2013) reported *U. canalensis* with umbones in a more anterior position, indicating a high morphological variability or alternatively the presence of two distinct species united in *U. canalensis*. Future work is needed to clarify if the morphologic variability among hitherto established species justifies species level separation. Furthermore, as outlined above, the generic assignment of Early Triassic *Unionites* species is still dubious in many cases.

Unionites canalensis was a shallow infaunal suspension feeder (Hautmann et al., 2013). Fürsich (1994) and Geyer et al. (2005) suggested that the genus is indicative of mesohaline conditions.

Unionites fassaensis (Wissmann *in* Münster), 1841
Figure 8.17, 8.18

1841 *Myacites fassaensis* Wissmann, 1841, p. 9, pl. 16, fig. 2a–2c.
1963 *Unionites fassaensis* (Wissmann); Ciriacks, p. 82, pl. 16, fig. 13.
?1963 *Unionites breviformis* (Spath); Ciriacks, p. 81, pl. 16, figs. 14, 15.
2009 *Unionites fassaensis* (Wissmann); Kumagae and Nakazawa, p. 167, figs. 144.5–144.9 (cum synonymis).

Description.—Shell equivalved, subelliptical in outline, with prosogyrate umbones projecting above dorsal margin. Beaks located approximately on anterior 40 percent or less of dorsal

margin. Ventral margin convex. Posterior margin blunt. Anterior margin rounded.

Material.—Recorded in great numbers throughout the formation. Predominantly preserved as external and internal molds. The description is based on some better preserved external molds from the sample GV-A-3 (PIMUZ 30542) and GV-B-1 (PIMUZ 30543).

Remarks.—*Unionites fassensis* is among the first re-colonizers after the end-Permian mass extinction and probably the most widely reported bivalve species from lower Triassic strata. The high morphological variability reported from this taxon, including its general form and the position of the beak (Kumagae and Nakazawa, 2009), may be an indication of a high intraspecific variability or, alternatively, of lumping together different species under this name.

Ecology is same as for *Unionites canalensis*.

Order Trigonioida Dall, 1889
Superfamily Trigoniacea Lamarck, 1819
Family Myophoriidae Bronn, 1849
Genus Neoschizodus Giebel, 1855
Neoschizodus laevigatus (Ziethen, 1830)
Figure 8.20

1830 *Trigonia laevigata*; Ziethen, p. 94, pl. 71, figs. 2, 6.
1963 *Myophoria laevigata* (Ziethen); Ciriacks, p. 82, pl. 18, figs. 18, 19.
2009 *Neoschizodus* cf. *laevigatus* (Ziethen); Kumagae and Nakazawa, p. 170, fig. 145.10–145.15.

Description.—Shell equivalved, moderately inflated, subtrigonal, slightly longer than high and inequilateral. Umbo orthogyrate, umbonal ridge straight and terminating towards almost straight posteroventral margin. Posterior margin truncated. Myophoric buttress well developed as indicated by the presence of a distinct diagonal groove anterior to the umbo.

Material.—Rarely recorded in the Gros Ventre Canyon sections. Two specimens in GV-A-3 and five specimens in GV-A-5 preserved as external molds. The description is chiefly based on the specimen PIMUZ 30545.

Remarks.—*Neoschizodus laevigatus* is a cosmopolitan species in Lower and Middle Triassic rocks. The high variability in its morphological parameters either results from a high intraspecific variation or from several poorly distinguishable taxa that were lumped under this species name. Accordingly, it is currently unclear whether the wide geographical range of this species is a true phenomenon or just an artifact of a poor species definition.

Neoschizodus laevigatus was a shallow infaunal suspension feeder (Hautmann et al., 2013).

Class Gastropoda Cuvier, 1797
Order Amphigastropoda Simroth, 1906
Superfamily Bellerophontoidea McCoy, 1852
Family Bellerophontidae McCoy, 1852
Genus Dicellonema Yü and Wang *in* Yü (1975)
Dicellonema abrekensis (Kaim, 2009)
Figure 8.21, 8.22

1899 *Bellerophon* sp. indet.; Bittner, p. 28, pl. 4, figs. 26–28.
2009 *Bellerophon abrekensis* sp. nov.; Kaim, p. 147, figs. 135, 136.
2010 *Bellerophon abrekensis* Kaim; Kaim et al., p. 123, fig. 2.
2011 *Dicellonema abrekensis* (Kaim); Kaim and Nützel, p. 191, fig. 1G.

Description.—Shell globular, slightly wider than long, with arcuate collabral ribs curved more posteriorly near the selenizone. Selenizone long and slightly raised.

Material.—Common in sample LPA-2. Description based on very few well preserved specimens (e.g., PIMUZ 30526).

Remarks.—*Bellerophon abrekensis* Kaim, 2009 was assigned to *Dicellonema* by Kaim and Nützel (2011) based on the presence of bundles of growth lines at the lateral borders of the selenizone. Kaim and Nützel (2011) considered this as a robust criterion for generic distinction between *Bellerophon* and *Dicellonema*, which was initially established as subgenus of *Bellerophon* (Yü and Wang, 1975) and raised to genus rank by Kaim and Nützel (2011). Well-preserved specimens from the Dinwoody Formation agree well with the characteristics of this species (Kaim, 2009; Kaim et al., 2010; Kaim and Nützel, 2011). *Dicellonema abrekensis* was probably a cosmopolitan species and is reported from western Panthalassa (Shigeta et al., 2009) and eastern Tethys (Kaim et al., 2010).

Dicellonema abrekensis was an epifaunal detritivor.

Order Caenogastropoda Cox, 1960
Family Coelostylinidae Cossmann 1909
Genus Coelostylina, Kittl, 1894
?Coelostylina sp. A
Figure 8.23

Description.—High-spired shells with up to four moderately expanding whorls. Sutures weakly incised. Protoconch and aperture not observed.

Material.—Rarely recorded in HS, GV-A-8, GV-A-5, LS-7, mostly very poorly preserved. The description is based on a small but comparatively well preserved specimen in sample HS (PIMUZ 30525).

Remarks.—The genus *Coelostylina* is probably the most widely reported gastropod genus from lower Triassic strata. This is mainly related to its shape providing little diagnostic criteria in combination with the general poor preservation of Early Triassic shelly fossils. For instance, juvenile specimens with few whorls developed may be easily confused with similar forms (e.g., *Omphaloptycha*) that lived during the same time interval (e.g., Kaim, 2009).

Coelostylina was an epifaunal detritivore (Schubert and Bottjer, 1995).

Brachiopoda Dumeril, 1806
Class Lingulata Goryansky and Popov, 1985
Order Linguilida Waagen, 1895
Family Lingulidae Menke, 1828
Genus Lingula Bruguiere, 1797
Lingula borealis Bittner, 1899
Figure 8.24

1899 *Lingula borealis* nov. sp.; Bittner, p. 25, pl. 4, figs. 1–7.
1942 *Lingula borealis* Bittner; Newell and Kummel, p. 953, pl. 2, figs. 1–4.

Description.—Shells elongately oval in outline, margins rounded; lateral margins subparallel, posterior parts of both valves weakly inflated along median longitudinal line. Shell surface generally smooth except for concentric fine growth lines.

Material.—Frequently recorded in the lower Dinwoody Formation (samples GV-B-B,HP-1, HP-3, HP-13, LS-5/a, LS-7, LS-5/b, LS-4/a, and CM). The description is based on some well preserved specimens recorded in the sample GV-B-B (e.g., PIMUZ 30546).

Remarks.—The specimens described herein agree very well with the type material of *L. borealis* of Bittner (1899). The other Early Triassic species *Lingula tenuissima* differs in having converging lateral margins. *Lingula borealis* has been frequently

reported in strata of the Panthalassa margin (Bittner, 1899; Rodland and Bottjer, 2001; Shigeta et al., 2009). The genus *Lingula* is extremely abundant in lower Triassic rocks and is the textbook example of a "disaster taxon", which became globally abundant in the aftermath of the end-Permian mass extinction.

Recent *Lingula* is a shallow infaunal suspension feeder.

Class Rhynchonellata, Williams et al., 1996
Order Terebratulida Waagen, 1883
Family Zeilleriidae Allan, 1940
Subfamily Zeilleriinae Allan, 1940
Genus Periallus Hoover, 1979
Periallus woodsidensis Hoover, 1979
Figure 8.25

1942 *Terebratula margaritowi* Bittner; Newell and Kummel, p. 954, p1. 2, fig. 5a, 5b.
1979 *Periallus woodsidensis* n. sp.; Hoover, p. 17, pl. 4, figs. 1–15.

Description.—Subpentagonal in outline, dorsal valve with faint median septum.

Material.—Locally abundant in the Terrace Mountain section (sample TM-4). The description is based on one well preserved specimen (PIMUZ30530).

Remarks.—The material at hand is rather poorly preserved and very few morphological criteria are observable. However, there is only a limited number of described articulate brachiopod species from the Lower Triassic, especially from Griesbachian and Dienerian rocks, which facilitates species identification. In the present case, terabratuliid brachiopods with median septa in the dorsal valve from the lower Triassic of the western U.S. have been referred to as *Periallus woodsidensis* (Hoover, 1979). In addition, the general outline agrees well with the figured material in Hoover (1979). The material figured by Newell and Kummel (1942), which was identified as *Terebratula margaritowi*, undoubtedly differs from the type material of Bittner (1899) in being wider than long. Hoover (1979) assigned their material to his new species, which is followed herein. The misidentification by Newell and Kummel (1942) may cause confusion with *Terebratula margaritowi*, which has been assigned by Dagys (1965) to *Fletcherina* (=*Fletcherithyris* Campbell, 1965). Hoover (1979) noted that *F. margaritowi* may, in fact, be closely related *P. woodsidensis*.

The stratigraphic occurrence of *Periallus* is incorrectly indicated as Olenekian by Chen et al. (2005), because it has repeatedly been reported in the Dienerian substage (post-*Claraia* beds in Newell and Kummel, 1942; Dinwoody and Woodside Formation in Hoover et al., 1979), but never in the Olenekian (Smithian and Spathian).

Periallus woodsidensis was a pedunculate epifaunal suspension feeder.

PALEOECOLOGY OF THE DINWOODY FORMATION

The results of the cluster analysis are shown in Figure 9. Absolute abundance data for all samples are provided in the online Supplemental file (see accessibility below; the grouped associations and assemblages with all relevant data can be found in Supplemental file worksheet, "Associations"). Seven associations (recurrent assemblages; Fig. 10) and four assemblages (sensu Fürsich, 1984) are recognized in the Dinwoody Formation. The assemblages and associations are characterized in the following. As outlined in the methods section, samples that were recognized in this study include beds with little evidence for transportation. Individual sample diversity refers to species richness.

Unionites fassaensis *association*.—This association (Fig. 10.1) is represented by the samples HS-1, GV-A-1, 2, 4, and GV-B-1, 2 and is dominated by *Unionites fassaensis*, which constitutes its trophic nucleus. *Unionites canalensis,* and *Promyalina spathi* are recorded in similarly small numbers. Individual sample diversity ranges from 1 to 3 (mean average=1.8). Dominance ranges from 0.81 to 1 (mean average=0.94). Two trophic guilds, epifaunal and shallow infaunal suspension feeders are recorded in this assemblage, each represented by two species. Infaunal suspension feeding bivalves are numerically dominant.

Association as well as individual sample diversity is very low and dominance values are very high, which may indicate environmental stress. The high proportion of siliclastic material and frequently observed convolute bedding in the host rocks suggests high sedimentation rates possibly accompanied by fluctuations in salinity caused the paucity of this fauna. Alternatively, taxonomic and ecologic pauperism of this association could simply be a result of the extinction because it is mainly composed of samples from the lower parts of the sections GV-A and GV-B, which are stratigraphically very close to the extinction event. All samples of this association are recorded in fine-grained, slightly calcareous sandstone.

Unionites fassaensis-Pteria ussurica *association*.—This association (Fig. 10.2) is recorded by the samples GV-B-3, GV-A-5 and LPA 2 and is dominated by the bivalves *Unionites fassaensis* and *Pteria ussurica*, which, together with the bellerophontid *Dicellonema abrekensis*, form the trophic nucleus. Additionally recorded are the bivalves *Promyalina putiatinensis, Promyalina spathi, Unionites canalensis, Neoschizodus laevigatus, Claraia mulleri, Claraia* cf. *stachei, Leptochondria occidanea, Myalinella postcarbonica,* and the gastropod *Coelostylina* sp. A. Individual sample diversity ranges from 2 to 9 (mean average=6). Dominance ranges from 0.25 to 0.51 (mean average=0.38). The ecological structure is relatively balanced with epifaunal- (seven species), endobyssate- (one species), and shallow infaunal (three species) suspension feeders as well as epifaunal detrivores (one species). The overall diversity, evenness and ecological structure suggest that this association represents relatively advanced recovery, with no indication of marked environmental stress.

All samples of this association occur in fine-grained marlstones. Shell size is variable in these beds, which suggests little reworking by waves. This association is present in the middle part of the Gros Ventre Canyon sections and in the Little Popo Agie Canyon. The presence of *Claraia mulleri* and *C*. cf *stachei* and the relatively narrow vertical range indicate that this association was present during a relatively short time interval straddling the Griesbachian-Dienerian boundary (see the chapter on the stratigraphy).

Unionites fassaensis-Lingula borealis *association*.—This association (Fig. 10.3) is represented by the samples CM and LS-4/a. The trophic nucleus is constituted by *Unionites fassaensis* and *Lingula borealis*. Additional species are *Promyalina spathi, Claraia aurita, Pteria ussurica*, *Unionites canalensis,* and *Myalinella postcarbonica*. Individual sample diversity is 5 and 6, respectively, and dominance 0.24 and 0.35. The ecological structure is quite balanced with four species of epifaunal-, three species of shallow infaunal, and one species of endobyssate suspension feeders present. However, shallow infaunal suspension feeders dominate numerically. This association is moderate in terms of diversity and ecological balance.

Eumorphotis multiformis *association*.—The *Eumorphotis multiformis* association (Fig. 10.4) is recorded by the samples HP-5, HP-2L, LS-7, LS-5/b, SC-1, and HS-L-1. *Eumorphotis multiformis, Lingula borealis, Eumorphotis* cf. *ericius,* and *Promyalina spathi* constitute the trophic nucleus. Additional species include *Unionites fassaensis, Eumorphotis amplicostata, Coelostylina* sp. A, *Unionites canalensis,* and *Pteria ussurica*. Individual sample diversity ranges from 1 to 8 (mean average=4.2). Dominance

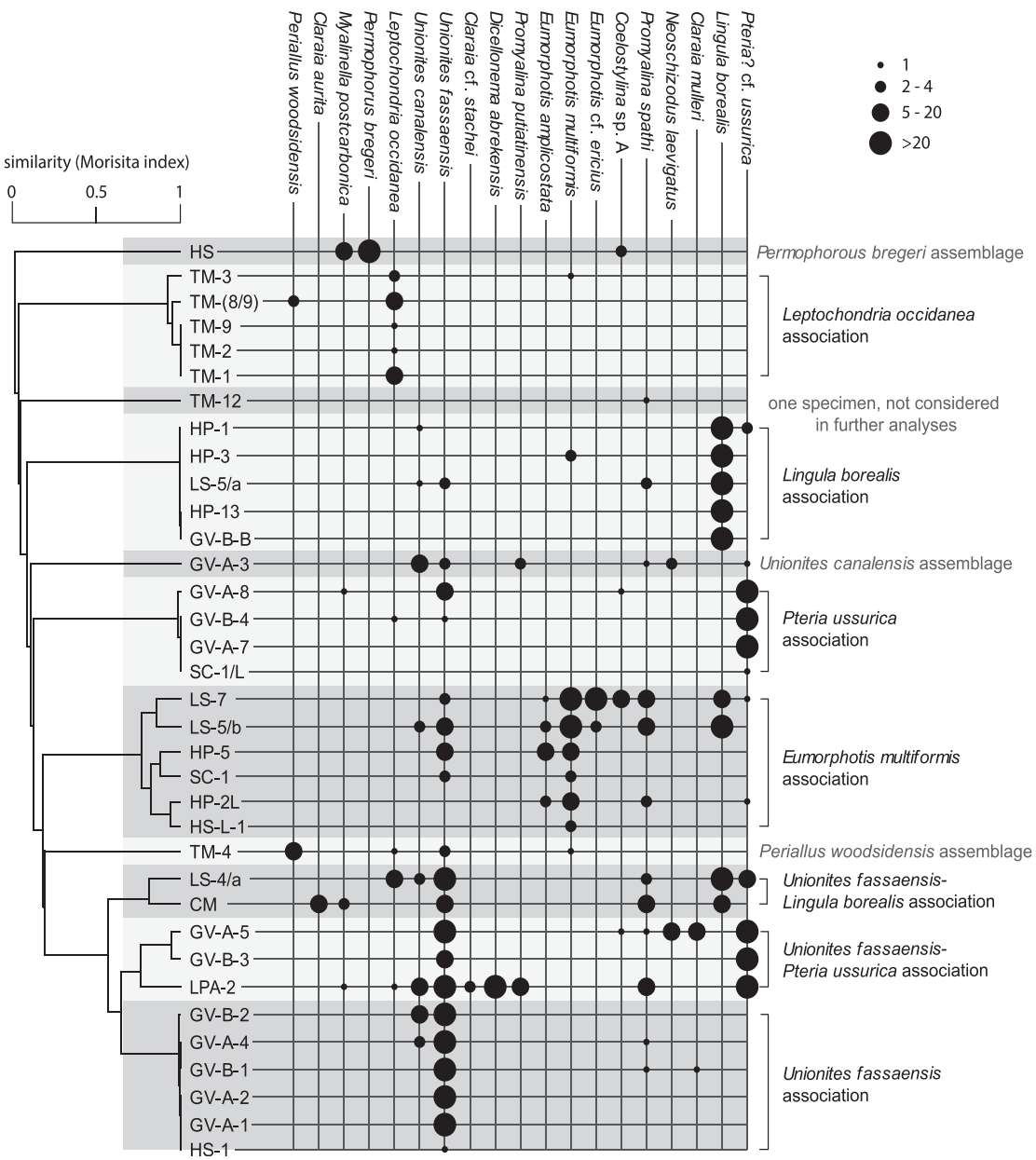

FIGURE 9—Results of the Q-Mode (samples) cluster analysis using the unweighted paired group algorithm and Morisita index of similarity. Classes of abundances (circle size) represent the quartiles of absolute-abundance frequencies.

ranges from 0.26 to 1 (mean average=0.51). However, two samples (SC-1, HS-L-1) with very low number of specimen cause underestimation of diversity and overestimation of dominance of the average values. Ecological guilds present in this association include epifaunal- (five species), shallow infaunal (three species), and endobyssate (one species) suspension feeders as well epifaunal detritivores (one species). However, in terms of numerical abundance, epifaunal and shallow infaunal forms clearly dominate.

The relatively high overall diversity, low dominance, and ecological heterogenity of this assemblage suggest that no pronounced environmental stress was present during deposition. Samples that constitute this assemblage are mainly derived from limestones of the sections of the Tendoy Range (LS, HP), where they are present over long lithostratigraphic ranges.

Pteria ussurica *association*.—The *Pteria ussurica* association (Fig. 10.5) is represented by the samples SC-1L, GV-A-7, GV-A-8, and GV-B-4 and is overwhelmingly dominated by this species. Other species include *Unionites fassaensis, Myalinella postcarbonica,* and *Coelostylina* sp. A, which are recorded infrequently. Individual sample diversity ranges from 1 to 4 (mean average=2.3). Dominance ranges from 0.79 to 1 (mean average=0.94). Ecological guilds present in this association include epifaunal suspension feeders (two species) as well as shallow infaunal-, endobyssate suspension feeders and epifaunal detritivores represented by one species each. However, endobyssate suspension feeders completely dominate in numerical

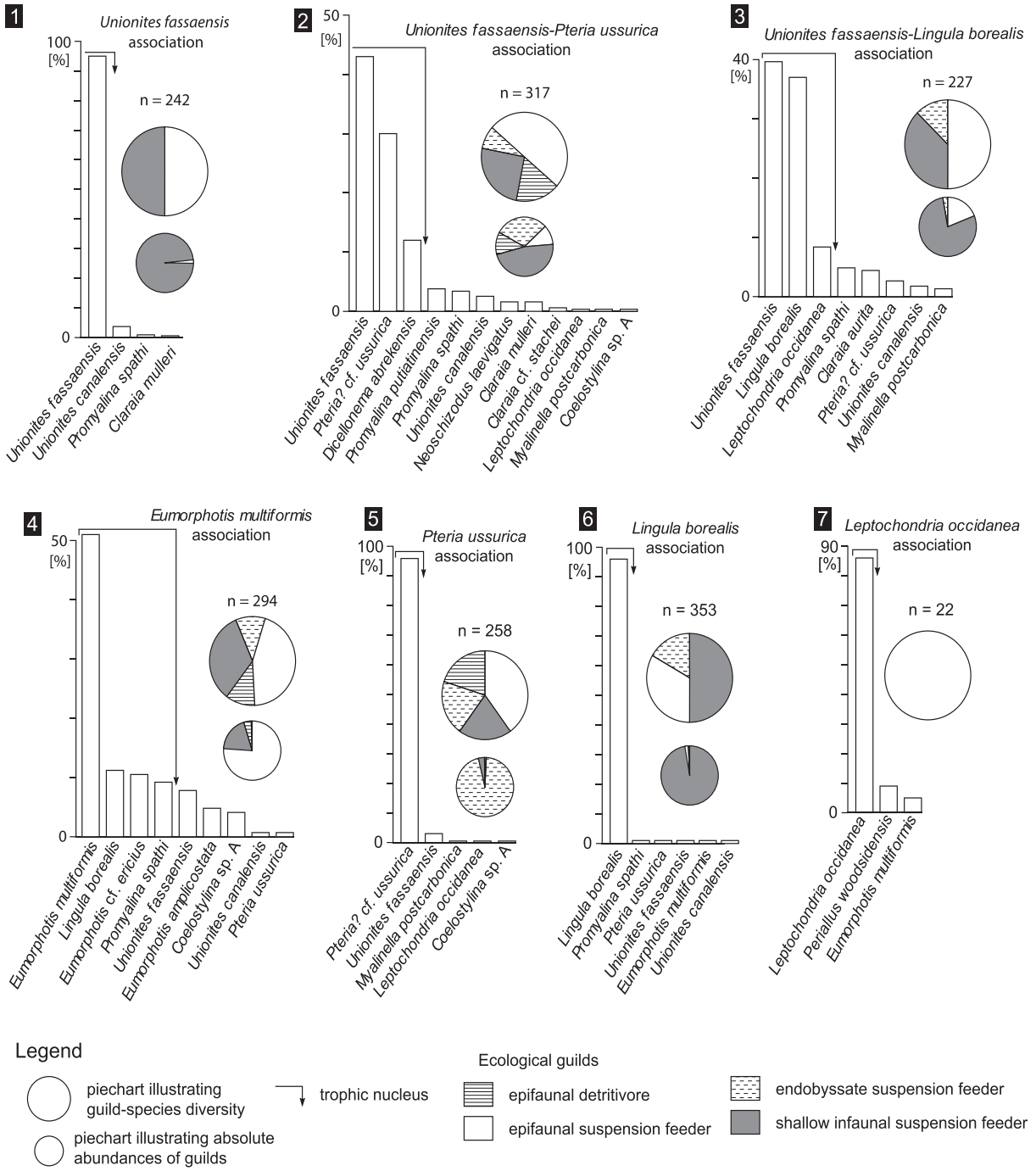

FIGURE *10*—Benthic associations recognized in the Dinwoody data set showing frequencies of identified fossils, the trophic nucleus, guild species diversity based on the number of species representing benthic guilds (large pie charts) as well as absolute abundance of guilds (small piecharts). These diagrams are based on merged samples that were grouped into one association in the cluster algorithm. *1*, *Unionites fassaensis* association; *2*, *Unionites fassaensis-Pteria ussurica* association; *3*, *Unionites fassaensis-Lingula borealis* association; *4*, *Eumorphotis multiformis* association; *5*, *Pteria ussurica* association; *6*, *Lingula borealis* association; *7*, *Leptochondria occidanea* association.

abundance. It seems that this association is a strongly depleted *Unionites fassaensis–Pteria ussurica* association and with its high dominance values and low diversities, it may indicate harsh or unstable environmental conditions. It could represent a decline in ecosystem stability after relatively balanced conditions recorded in the samples in the middle part of the Formation at the same localities.

Lingula borealis *association*.—This association (Fig. 10.6) is recorded by the samples GV-B-B, HP-13, HP-3, HP-1, and LS-5/a. It is dominated by *Lingula borealis*. Other species in this

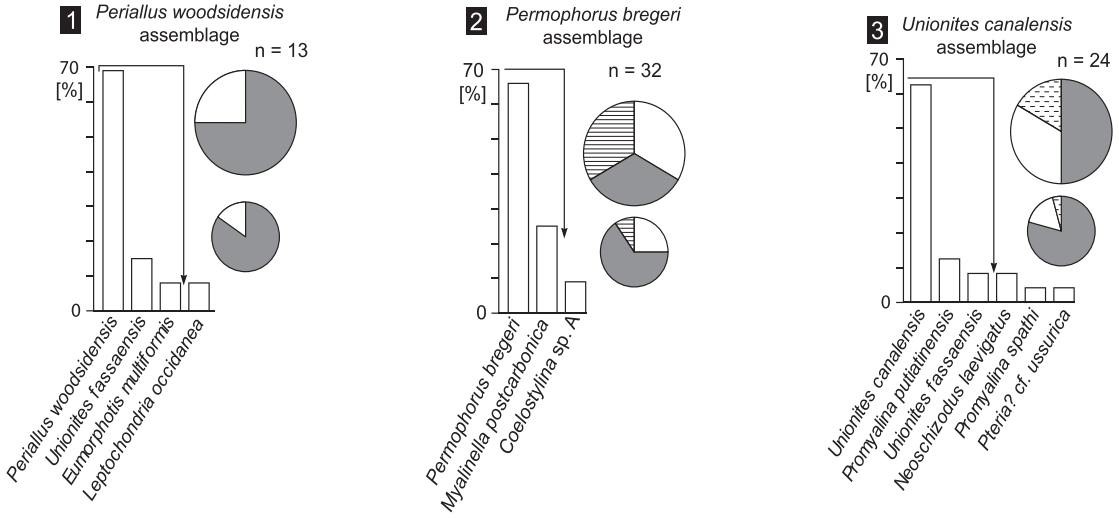

FIGURE *11*—Benthic assemblages that were not assigned to associations in the cluster algorithm. See Figure 10 for legend and explanations. *1*, *Periallus woodsidensis* assemblage; *2*, *Permophorus bregeri* assemblage; *3*, *Unionites canalensis* assemblage.

association are *Eumorphotis multiformis, Pteria ussurica*, *Unionites fassaensis, Unionites canalensis, Promyalina spathi* but these are numerically of minor importance. Individual sample diversity ranges from 1 to 4 (mean average=2.2). Dominance ranges from 0.87 to 1 (mean average=0.93). Ecological guilds include shallow infaunal (three species), epifaunal (two species) and endobyssate (one species) suspension feeders. It terms of absolute abundance, shallow infaunal suspensions feeder are overwhelmingly dominant. The high dominance values, low diversities, and the ecological structure, which is dominated by infaunal suspension feeders, is suggestive of stressed conditions, which may characterize the siliclastic siltstone to very fine-grained sandstone facies in which *Lingula borealis* commonly occurs.

Alternatively, the ecological parameters and low diversity may be related to the stratigraphical proximity to the mass extinction level, because this association is preferentially recorded in the lower parts of the sections GV-B, HP and LS.

Leptochondria occidanea *association*.—The *Leptochondria occidanea* association (Fig. 10.7) is exclusively recorded by the samples from the section TM and dominated by this species, which forms its trophic nucleus. Accessory species are *Eumorphotis multiformis* and *Periallus woodsidensis*. Due to poor preservation and very little sample material, the number of specimens is not very high and ecological indices are probably not very significant. Sample diversity is 1 or 2 (mean average=1.4) and dominance values range from 0.63 to 1 (mean average=0.86). The group of epifaunal suspension feeders is the only ecologic guild present in this association. The high dominance values, low diversities, and the impoverished ecological structure indicate unstable conditions but, as already noted, the low number of sampled specimens in this section makes any interpretation tentative only.

Periallus woodsidensi*s assemblage*.—Sample TM-4 constitutes this assemblage (Fig. 11.1) and contains *Periallus woodsidensis*, *Unionites fassaensis, Eumorphotis multiformis,* and *Leptochondria occidanea*. Species richness is four and dominance is 0.51. The allocation of this assemblage within the cluster analysis appears surprising since this sample is not fundamentally different from samples that clustered in the *Leptochondria occidanea* association. Accordingly, this assemblage is very similar to the ecological characteristics outlined in the paragraph above.

Permophorus bregeri *assemblage*.—The trophic nucleus of this assemblage (sample HS; Fig. 11.2) is represented by *Permophorus bregeri* and *Myalinella postcarbonica Coelostylina* sp. A is a minor component of this assemblage. The dominance is 0.50. *Myalinella postcarbonica* is an epifaunal- and *Permophorus bergeri* a shallow infaunal suspension feeder. *Coelostylina* sp. A is an epifaunal detritivor. All three ecologic guilds are represented by one species each. The absolute abundance numbers indicate the dominance of shallow infaunal suspension feeders. As noted in the discussion on *Permophorus bregeri*, this species appears to be unique to sections in southeastern Idaho and, thus, the isolated position in the cluster analysis could reflect a paleogeographic signal.

Unionites canalensis *assemblage*.—The *Unionites canalensis* assemblage (Fig. 11.3) is represented by the sample GV-A-3 and its trophic nucleus is composed of *Unionites canalensis, Promyalina putiatinensis,* and *Unionites fassaensis*. Additional occurrences include *Promyalina spathi, Pteria ussurica*, and *Neoschizodus laevigatus*. Species richness is six and dominance is 0.42. This sample is very similar to the *Unionites fassaensis–Pteria ussurica* association, and all ecological characteristics outlined in the corresponding paragraph apply to this association, too.

Ichnology.—Trace fossils (Fig. 12) were not systematically sampled and a lengthy discussion is beyond the scope of this

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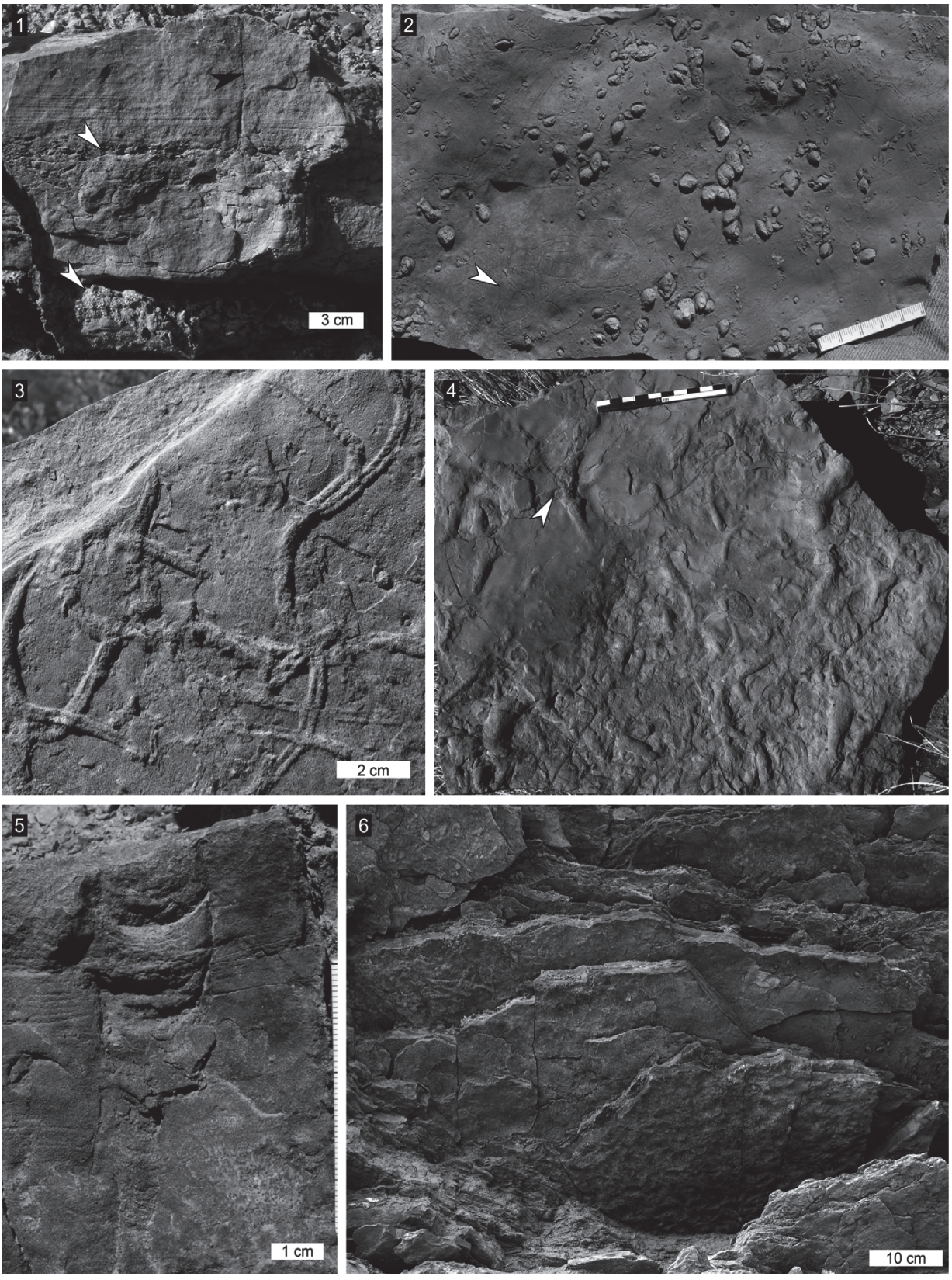
Figure *12*—Trace fossils of the Dinwoody Formation. *1*, *Skolithos linearis* (black arrow) in laminated sandstones with truncated top; note the pervasively bioturbated intervals (white arrows); *2*, *Lockeia* isp. (positive hyporelief) and *Gordia marina* (negative hyporelief, white arrow), a typical ichnoassemblage of the middle Dinwoody Formation as recorded in section HP; *3*, *Gyrochorte* cf. *comosa* as positive epirelief in fine-grained sandstones of the upper Dinwoody Formation at section HP; *4*, pervasive horizontal bioturbation in lower bedding plane view dominated by *Palaeophycus tubularis* and questionably *Thalassinoides* isp. (wide arrow); *5*, retrusive *Diplocraterion* isp. seen in full relief in siltstone in the lower part of section HS; *6*, exposed lower bedding planes revealing abundant horizontal bioturbation, middle section HP.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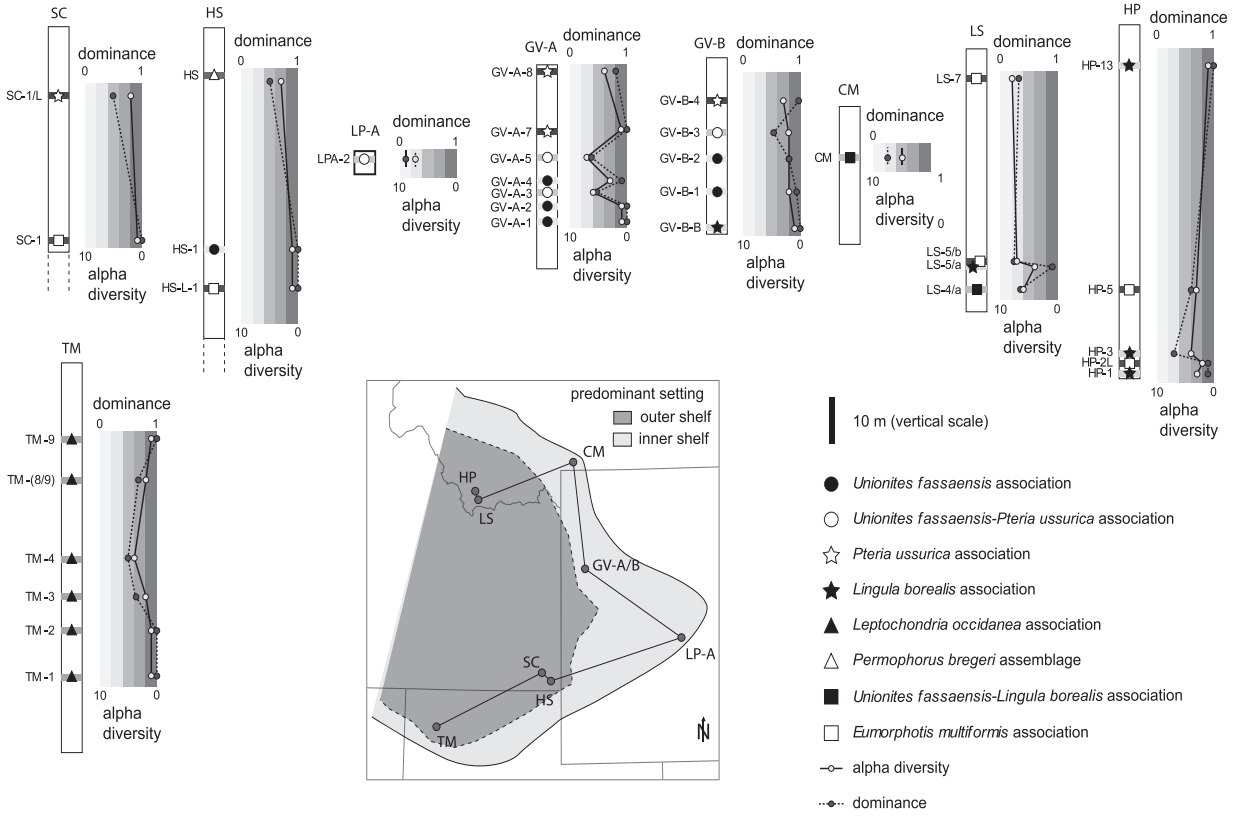

FIGURE *13*—Comprehensive compilation of diversity, dominance and associations to depict spatial and temporal trends within the Dinwoody Formation. Columns height represents scaled stratigraphic thicknesses. Dashed lines below the columns indicate that unsampled parts of the sections are excluded to maintain graphic lucidity. For lithological information and precise sample levels see Figures 2, 4, and 5. Arrangement of sections follows the transect indicated on the locality map.

paper, but some general observations are worth being added here. Intensive bioturbation (Fig. 12.1) is rarely observed and in most parts of the sections and even scarce biogenic sediment reworking is rare. However, exposed bedding planes (Fig. 12.4, 12.6) of virtually unbioturbated strata revealed that horizontal epifaunal and shallow tier trace fossils such as *Asteriacites, Gordia* (Fig. 12.2), *Gyrochorte* (Fig. 12.3), *Lockeia* (Fig. 12.2), *Palaeophycus,* and *Planolites* may be abundant. Vertical bioturbation is represented by *Arenicolites, Diplocraterion* (Fig. 12.5), and *Skolithos* (Fig. 12.1), which are more frequently observed in the middle part of the Hot Springs, Sleight Canyon, Little Sheep Creek, and Hidden Pasture sections. The trace fossils indicate a very simple tiering structure which is dominated by epifaunal and shallow infaunal detritus feeders (*Planolites, Gyrochorte, Gordia*) and epifaunal to infaunal suspension feeders (*Arenicolites, Diplocraterion, Lockeia, Palaeophycus* and *Skolithos*). Additionally, *Asteriacites* and *Palaeophycus* indicate the presence of epifaunal to shallow infaunal carnivores or scavengers.

Summary.—In general, the ecological structure of the Dinwoody fauna is very simple. In the shelly fauna, epibysally attached, endobyssate, and shallow infaunal suspension feeders as well as epifaunal detritus feeders are recognized, which sums up to four out of 13 typically Mesozoic benthic guilds (cf. Aberhan, 1994). In most samples, epifaunal and shallow infaunal bivalves form the main constituents. *Lingula* or *Pteria* are locally dominant. The trace fossils add three more benthic guilds (shallow infaunal detritus feeders, infaunal suspension feeders, and epifaunal or shallow infaunal carnivores) to the list. With bivalves, gastropods, and inarticulate brachiopods, only three marine invertebrate classes are recorded. Apart from a single specimen of the ophiurid resting trace *Asteriacites* observed in section LPA, echinoderms are absent. Trace fossil/trace maker relationships of remaining trace fossils mentioned above are too equivocal to reliably conclude on the presence of particular soft-bodied marine invertebrates in the Dinwoody Formation.

SPATIAL AND TEMPORAL TRENDS

Apart from ecological conditions, the diversity, taxonomic composition, and ecological structure of paleocommunities is, to a varying extent, also controlled by age (stratigraphic level) and paleogeography. Although trends are not very distinct in the Dinwoody data set and a poor age control hampers precise correlation of samples, detailed analyses reveal some insight into recovery dynamics of the Early Triassic marine ecosystems in the western U.S. Trends of alpha-diversity, dominance of samples and the spatial distribution of the benthic associations are summarized in Figure 13.

Ecology structure and diversity through time and space.—There is a considerable stratigraphical gap between Permian and Triassic rocks. Accordingly, the actual extinction horizon is not recorded in the study area. Strata of the basalmost Dinwoody Formation (Fig. 13) contain paucispecific associations such as the *Unionites fassaensis* and the *Lingula borealis* association, which both are characterized by very few numerically dominant taxa and a very simple ecology with one guild being highly dominant. In these beds, the *Eumorphotis multiformis* association (Fig. 14.1) is also represented by low-diverse samples.

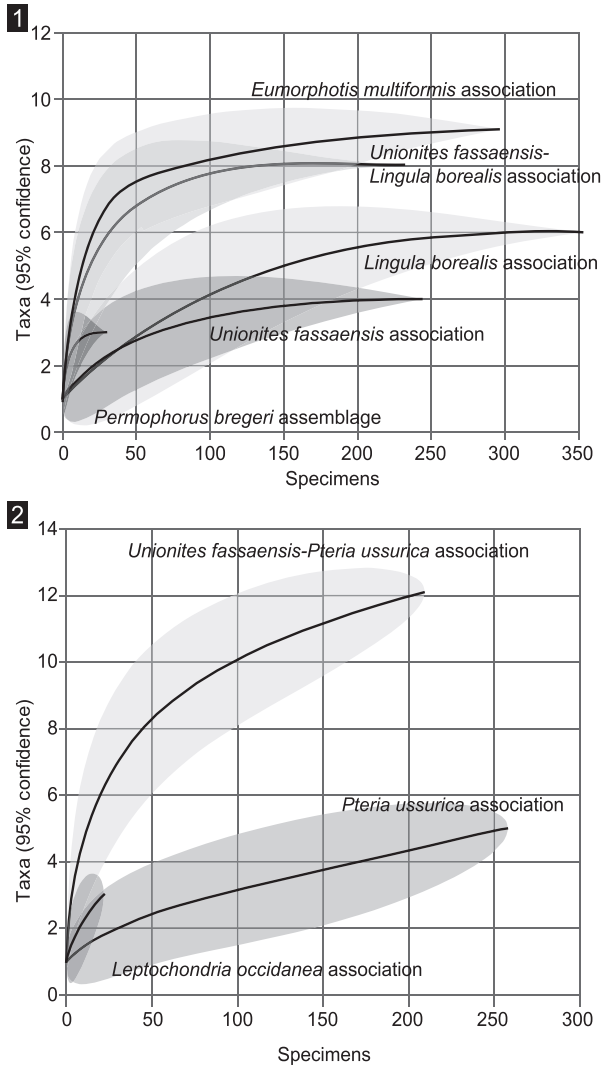

FIGURE *14*—Rarified alpha diversities for the associations identified in the data set. *1*, associations which level off, indicating that further sampling effort would have had no significant impact on alpha diversities; *2*, associations with more open rarefaction curves indicating that further sampling would have added more species and thus indicates that alpha-diversity values for these associations are tentative.

In the middle part of the sections LPA, GV-A/B, HP and LS, faunas considerably increase in diversity with up to nine species recorded in single samples and up to 12 species present in the fairly diverse *Unionites fassaensis–Pteria ussurica* and the *Eumorphotis multiformis* associations. Both associations and constituting samples also exhibit the lowest dominance values (D=0.25) of the whole dataset. Furthermore, these communities indicate balanced ecological conditions with several ecological guilds occurring in similar abundances (see Fig. 10). The *Pteria ussurica* association of the sections GV-A/B documents a huge decline to very low diversities and high dominance values higher in the sections. The sections of outer shelf settings, i.e., HS, SC, and TM, show no marked differences in diversity and dominance through time and all samples are characterized by low diversity–high dominance communities. This could indicate that water depth and paleogeography have had an effect on the ecological structure and diversity. However, samples from these intervals are low in specimen number, and the rarefaction curves of corresponding associations (Fig. 14.2) suggest that diversity values may suffer from undersampling. Accordingly, any interpretation needs to be substantiated by more data.

Rarefaction analyses of the associations reveal sufficient sampling effort in most other cases (Fig. 14.1), with exception of the *Unionites fassaensis–Pteria ussurica* association (Fig. 14.2). This, however, would only corroborate its status as the most diverse association. Also the rarefaction curves of the *Leptochondria occidanea* and *Pteria ussurica* associations indicate that additional sampling would have added significantly more taxa (Fig. 14.2). The samples constituting the *Leptochondria occidanea* association are in fact charactized by a very low specimen number and it cannot be excluded that this low-diversity signal from the section TM is mainly due to poor sampling density and preservation. The *Pteria ussurica* association is comparatively well sampled and we do not expect that increased sampling would have increased alpha-diversity to a level comparable to more diverse association.

Ichnological data more or less mirror the trend seen in diversity data. Most of the trace fossils mentioned above represent domichnia and thus indicate normal marine, oxygenated conditions (e.g., Savrda and Bottjer, 1986; Ekdale and Mason, 1988). Trace fossils are particularly abundant in the middle part of the sections HP, LS and LPA.

In summary, the Dinwoody Formation is dominated by typical post extinction faunas, which are characterized by low diversity, low ecological guild diversity, and high dominance. Relatively diverse communities (for Early Triassic standards; cf. Schubert and Bottjer, 1995) are present in inner shelf deposits and restricted to the middle part of the Dinwoody Formation. Based on the occurrence of the species *Claria* cf. *stachei* and *Claraia mulleri* in the corresponding associations, this signal seems to occur around the Griesbachian–Dienerian boundary interval.

Paleogeographic variations.—It has been suggested that Early Triassic faunas had vast spatial ranges and that the portion of wide-ranging taxa on a basinal and interregional scale was generally high, at least on the genus level (Schubert and Bottjer, 1995; but see Wasmer et al., 2012). However, the portion of taxa that are unique to few associations is quite high in the Dinwoody Formation (Fig. 15), indicating some partitioning with respect to stratigraphic level or paleogeography. Figures 9 and 13 show that this partitioning mirrors spatial differences rather than stratigraphic signals, possibly due to a combination of facies effects and geographically restricted occurrences of taxa, e.g., communities which are dominated by *Unionites* are more typically recorded in deposits with a high portion of siliclastic material. As already pointed out in the discussion on the corresponding associations, this could express the tendency of this genus to tolerate salinity fluctuations (Fürsich, 1993; Geyer et al., 2005), which might have accompanied the deposition of terrigenous material. However, some associations also tend to be restricted to geographic regions. Wyoming sections mainly host the *Unionites fassensis–Pteria ussurica* and the *Pteria ussurica* associations. The *Eumorphotis multiformis* association is well developed in the section of Montana and Idaho. The *Leptochondria occidanea* association is unique to northwestern Utah. However, especially the latter association probably suffers from low sampling density and low outcrop area as well as generally bad preservation at this locality. Such secondary effects may account for this pattern. A comparison with the fauna of Virgin Formation, which exhibits a low beta-diversity (Hofmann et al., 2013), furthermore shows that beta-diversity is still comparably low in Dinwoody Formation (see online Supplemental file, Excel sheet "diversity" and discussion below).

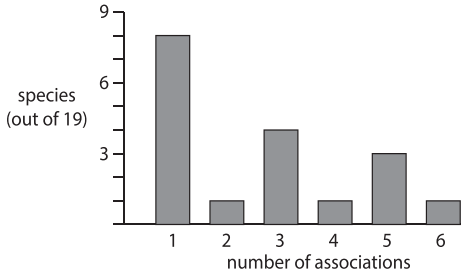

FIGURE 15—Graph illustrating the endemicity of the fauna. The height of the bars indicates how many species occur in how many associations. The more the spectrum is shifted towards the left, the higher is the rate of taxa that are unique to few associations.

DISCUSSION

The Griesbachian and Dienerian substages represent the immediate aftermath of the end-Permian mass extinction. The established geochronological framework for the Early Triassic (Mundil et al., 2004; Ovtcharova et al., 2006; Galfetti et al., 2007) suggests that these two substages span a time interval of less than 1.5 million years. Faunas of this time interval, and generally of the entire Early Triassic, were suggested to be of low ecological complexity, low diversity, high dominance, and a high proportion of so-called disaster species and cosmopolitan taxa (Schubert and Bottjer, 1995; Hallam and Wignall, 1997). Recent analyses (e.g., Krystyn et al., 2003; Hautmann et al., 2011; Hofmann et al., 2011) show that faunas with comparatively high diversities and low dominance values occurred at least locally, suggesting that benthic recovery was either diachronous in different paleogeographic regions (e.g., Twitchett and Barras, 2004; Twitchett et al., 2004), or that the restoration was well under way on an interregional scale significantly earlier than generally assumed (Hautmann et al., 2011; Hofmann et al., 2011). Accordingly, a continuous documentation of recovery throughout this time interval is important for testing each of these two scenarios. The Lower Triassic of the western United States represents a key area because it holds the most continuous record of a low-latitude setting from eastern Panthalassa of that time interval.

The benthic paleoecology of the Dinwoody Formation has been studied rather peripherally in Schubert and Bottjer (1995), who focused on a much broader stratigraphic and spatial scale. Schubert and Bottjer (1995) suggested that the Dinwoody communities are "characterized by very high dominance, low diversity assemblages consisting primarily of potential disaster forms, *Lingula* and *Claraia*". In contrast, Schubert and Bottjer (1995, appendix 3) indicated nine genera of benthic organisms in the ecologically quite even samples "D3" and "D4", which in terms of diversity and evenness overlap with more advanced faunas from the Sinbad and Virgin Formation presented in the same study. Nevertheless, the survey of Schubert and Bottjer (1995) together with some later studies (e.g., Twitchett and Wignall, 1996; Pruss and Bottjer, 2004) consolidated the view that deleterious environmental conditions persisted well into the Early Triassic (Wignall and Hallam, 1992) and, hence, were most likely responsible for a delayed recovery. The analysis presented herein allows us to reconstruct recovery patterns of Griesbachain and Dienerian benthic faunas of the western U.S. in more detail and to evaluate the recovery status and the influence of environmental stress.

Recovery patterns.—Ecological guild diversity, alpha-diversity and dominance of taxa are parameters that are generally used to define recovery stages (e.g., Schubert and Bottjer, 1995; Twitchett et al., 2004; Twitchett, 2006; Hofmann et al., 2011). According to the criteria of Twitchett (2006, fig. 3), incipient recovery occurred at least in inner shelf habitats of the Dinwoody basin around the Griesbachian–Dienerian boundary interval. This is indicated by sample diversities of up to nine taxa (and more in associations), comparatively large diameters of burrows (more than 2 cm) and large-sized shelly fossils (up to 6 cm sized bivalves) as well as locally abundant vertical bioturbation. Benthic communities thus reached a recovery stage that was previously not expected for equatorial regions of eastern Panthalassa during this time interval (Twitchett and Barras, 2004). Moreover, the Dinwoody fauna supports the hypothesis of an interregional recovery signal around the upper Griesbachian and lower Dienerian time interval (Hautmann et al., 2011; Hofmann et al., 2011) in benthic communities.

In contrast to late Griesbachian/early Dienerian faunas of inner shelf settings, most samples from outer shelf settings and from the basal part of the Dinwoody Formation show a significant lower diversity. Wignall and Hallam (1992) suggested that outer shelf deposits of the Dinwoody Formation were accumulated under anoxic and dysoxic conditions and hypothesized that oxygen deficiency was one of the main factors to delay the recovery from the end-Permian mass extinction. The spatial trends outlined herein do not contradict this idea at least for the deeper part of the basin, but they are also in accordance with alternative explanations. The low diversity could reflect locally insufficient sample density and low specimen numbers. As outlined earlier, the *Leptochondria occidanea* association (Fig. 14.2) might have been insufficiently sampled and, thus, its true diversity has been underestimated. However, rarefaction curves of all other low diverse associations (Fig. 14.1) indicate sufficient sampling, which suggests that the general pattern outlined above is real.

Apart from oxygen deficiency, other local stress factors such as salinity fluctuations and continental run-off could have had influenced diversity, dominance, body size, bioturbation, and tiering, which were previously used as parameters for characterizing recovery stages (Twitchett, 2006, fig. 3). The low diverse *Unionites fassaensis* and *Lingula borealis* associations are exclusively recorded in siliclastic units. The former is typically associated with beds indicating high sedimentation rates. The genus *Unionites* is known to occur in brackish water settings (Fürsich, 1993; Geyer et al., 2005). *Lingula* forms mass occurrences in massive fine-grained sandstones and shales, which both testify a high input of terrestrial material. Accordingly, both associations could correspond to periods of high siliclastic input, which were likely associated with fluctuations in salinity. The rarity of stenohaline taxa such as echinoderms and ammonoids in the Dinwoody basin lends some support for this hypothesis. Similarly, Schulbert and Nützel (2005) suggested that the stressed communities of the Dienerian Gastropod Oolith Member of the Werfen Formation (Dolomites, Italy) likely reflect local fluctuations in salinity. However, freshwater input from continental sources would result in a gradient of increasing salinity from the margin of the basin towards its center, a trend that is not in accordance with the diversity increase in the opposite direction (from the center to the margin) observed in the later interval of the Dinwoody Formation. This limits the application of a reduced salinity scenario to the basal part of the Dinwoody Formation.

Another possible explanation of the low diversity of outer shelf communities is that this pattern is simply not unusual. Miller (1988) demonstrated that bivalves have shown a comparable onshore–offshore diversity trend throughout the Phanerozoic of northern America. If this diversity pattern is continuously observed throughout time intervals with no marked extinctions, the same trend cannot be considered as diagnostic for extinction

aftermaths and moreover, is not a robust indicator of unusual environmental stress. Furthermore, it is well established that near shore environments typically host first order evolutionary innovations in benthic faunas before they expand offshore (Jablonski et al., 1983; Bottjer et al., 1996). Accordingly, the relevance of low-diverse offshore faunas in the Early Triassic might have been greatly overestimated in the discussion of tempo and affecting factors of recovery processes.

Returning to the prevalence of depauperated associations recorded in the lowermost Dinwoody Formation (i.e., the *Lingula borealis* and the *Unionites fassaensis* association, Fig. 13), the most straightforward explanation is that these simply reflect the immediate outcome of the extinction event itself, rather than the persistence of unusual conditions. Eurytopic genera such as *Lingula* (Rodland and Bottjer, 2001) and *Unionites* can quickly proliferate when ecospace is vacant and no specialized taxa compete. Conversely, the diversity rise in the younger interval of the Dinwoody Formation is most likely caused by the establishment of more specialized species, which outcompete pioneering generalists as they successively reappeared after the extinction (e.g., "preadapted survivors" of Kauffman and Harries, 1996). In the Dinwoody Formation, possible candidates are taxa such as *Promyalina putiatinensis, Eumorphotis amplicostata,* or *Leptochondria occidanea*. These species are rare in sum but contribute to higher diversities in some samples. All of them are attached epifaunal suspension feeders. The competitive advantage of these species in comparison to the two infaunal species *Lingula borealis* and *Unionites fassaensis* could be a more efficient filter feeding (Cranford and Grant, 1990; McRoberts and Newton, 1995). These, or closely related species became also widely established in the Spathian Virgin Formation, which records normal marine conditions (Hofmann et al., 2013). Accordingly, their appearance in the Dinwoody Formation makes persistent environmental stress rather unlikely.

Summarized, the low diversity of post-extinction faunas does not necessarily require unusual environmental conditions or ubiquitous stress (Hallam, 1991; Wignall and Hallam, 1992). Alternative explanations include 1) sampling bias, 2) local facies effects, 3) normal onshore-offshore trends, and 4) the immediate outcome of the extinction event itself. For the Dinwoody Formation, particularly the scenarios 3 and 4 challenge previous models of oxygen deficiency as the major driver of diversity pattern.

Trends in alpha- and beta-diversity.—Hofmann et al. (2013) proposed that trends in alpha-diversity (within-habitat diversity) and beta-diversity (between-habitat) provide a potential tool for discriminating between two recovery stages, the first ending with habitat saturation and the second ending with completion of ecosystem differentiation. "Undersaturated" ecosystems that prevail in the first recovery phase are characterized by a low degree of competitive exclusion simply because the number of competing species was low. In this situation, the need for resource partitioning, e.g., by separation along environmental gradients, is lower than in background times, and species may be able to exist through the full range of their fundamental niches. Accordingly, a relatively low beta-diversity is predicted as being indicative for undersaturated ecosystems. The scenario of ecosystem undersaturation offers an intrinsic explanation for the wide environmental range of taxa in the aftermath of the end-Permian mass extinction as an alternative to previous models that hypothesized the persistence of harsh environmental conditions (Pruss and Bottjer, 2004; Boyer et al., 2004; Mata and Bottjer, 2011). The stage of ecosystem undersaturation ends when diversity has increased by origination and/or immigration of new taxa to a level where competition urges species into their ecological optimum, thereby increasing beta-diversity.

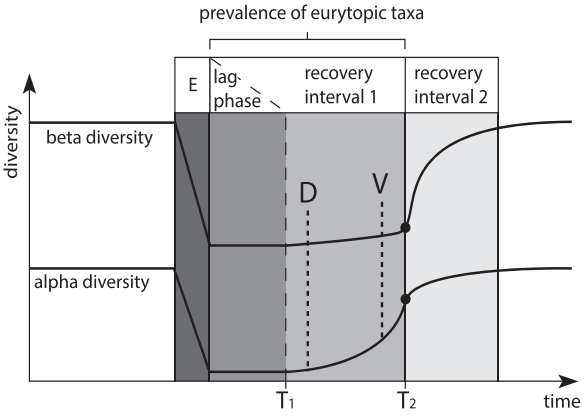

FIGURE *16*—Generalized model (Hofmann et al., 2013) illustrating the role of habitat saturation in recovery processes. The drop of alpha-diversity in course of an extinction (E) leads to a corresponding loss of beta-diversity and a highly reduced competition among species. A lag phase marks a time interval in which no significant radiation and increase in alpha-diversity is observed (Erwin 2001). After initial diversification (T1, start of recovery interval 1), competition within habitats increases following recovering alpha-diversity. Beta-diversity remains low throughout this interval because adding new species does not result in significant competition for resources. Eventually, alpha-diversity reaches a threshold value where a critical number of species competes for same, limited resources. The time when this habitat saturation is reached is herein referred to as T2. From this time onward (recovery interval 2), species are increasingly restricted to particular niches because of competitive exclusion from neighbouring habitats. Recovery interval 2 ends when all curves level off. Logistic growth of alpha-diversity is adopted from Erwin (2001). The data from the Dinwoody Formation suggest that alpha-diversity is lower than in the Virgin Formation (Hofmann et al., 2013) whereas beta-diversity is low in both units.

The Dinwoody fauna offers a first opportunity for a comparison of alpha- and beta-diversity between Griesbachian to early Dienerian (this study) and Spathian (Hofmann et al., 2013) ecosystems of the western United States. Calculations of beta diversities for both Formations is provided in the online Supplemental file (Excel sheet "Diversity"). Mean alpha-diversity is lower in the Dinwoody Formation (6.7 species) than in Virgin Formation (13 species). Using the mean minimum beta-diversity approach outlined in the methods section, we find that beta-diversity of the Dinwoody fauna (mean maximum Jaccard coefficient of similarity=0.44) is similar to that of the Virgin fauna (mean maximum Jaccard coefficient of similarity =0.48), based on the data of Hofmann et al. (2013). The slightly higher beta-diversity (lower Jaccard coefficient) for the Dinwoody fauna is probably due to the much larger geographical extent of the sampled area and to the longer stratigraphical interval covered by the samples. These new data are therefore in accordance with the hypothesis that beta-diversity was generally low in Early Triassic ecosystems and that alpha-diversity increase precedes beta-diversity increase (Fig. 16). Between-habitat differentiation (recovery interval 2 in Fig. 16) is, thus, a Middle to Late Triassic affair, possibly fostered by increased competition.

In summary, the data of the Dinwoody Formation is in accordance with the model of Hofmann et al. (2013), which suggests that the wide environmental and geographic range of taxa is an intrinsic effect of post-extinction faunas and thus does not necessarily reflect deleterious environmental conditions.

CONCLUSIONS

Our quantitative paleoecological analysis of the benthic fauna of the Dinwoody Formation reveals that outer shelf environments and the basal part of inner shelf environments were

dominated by low diverse/high dominance associations. In contrast, inner shelf environments of the middle part of the Dinwoody Formation record comparably diverse communities with low species dominance. We infer that moderate recovery was possible at the tropical eastern margin of Panthalassa. This observation supports recent evidence for a first interregional recovery pulse around the Griesbachian–Dienerian boundary interval. The low diversity recorded in outer shelf settings is possibly not fundamentally different from comparable onshore-offshore trends in background times. The low diversity in inner shelf settings at the base of the formation most likely results from the intensity of the mass extinction itself, possibly added by local environmental stress such as reduced salinity. The Dinwoody fauna is characterized by low beta-diversity and, hence, little faunistic differentiation between habitats. This finding supports the scenario of ecologically undersaturated Early Triassic ecosystems (Hofmann et al., 2013), which temporarily allowed species to exploit unusual wide environmental and geographic ranges. Important features of post-extinction faunas such as the wide environmental range of surviving taxa and the dominance of "disaster" species may thus express intrinsic traits of ecosystems that have been affected by a mass extinction event.

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ACCESSIBILITY OF SUPPLEMENTAL DATA

Supplemental data deposited in Dryad repository: http://dx.doi.org/10.5061/dryad.5mg73.

REFERENCES

Aberhan, M. 1992. Palökologie und zeitliche Verbreitung benthischer Faunengemeinschaften im Unterjura von Chile. Beringeria, 5:3–174.

Aberhan, M. 1994. Guild–structure and evolution of Mesozoic benthic shelf communities. Palaios, 9:516–540.

Aberhan, M. and H. Muster, 1997. Palaeobiology of Lower Jurassic bakevelliid bivalves from western Canada. Palaeontology, 40:799–815.

Allan, R. S. 1940. Studies on the Recent and Tertiary Brachiopoda of Australia and New Zealand. Canterbury Museum Records, 4:231–297.

Amalizky, W. 1892. Ueber die Anthracosien der Permformation Russlands. Palaeontographica, 39:125–213.

Beatty, T. W., J. P. Zonneveld, and C. M. Henderson. 2008. Anomalously diverse Early Triassic ichnofossil assemblages in northwest Pangea: s case for a shallow-marine habitable zone. Geology, 36:771–774.

Begg, J. G. and H. J. Campbell. 1985. *Etalia*, a new Middle Triassic (Anisian) bivalve from New Zealand, and its relationship with other pteriomorphs. New Zealand Journal of Geology and Geophysics, 28:725–741.

Beurlen, K. 1944. Beiträge zur Stammesgeschichte der Muscheln. Sitzungsberichte der Bayerischen Akademie der Wissenschaften, 1–2:133–145.

Bittner, A. 1891. Triaspetrefakten von Balia in Kleinasien. Jahrbuch der k. k. Geologischen Reichsanstalt, 41:97–116.

Bittner, A. 1899. Trias–Ablagerungen des Süd–Ussuri–Gebietes in der ostsibirischen Küstenprovinz. Mémoires du Comité Géologique, 7:1–35.

Bittner, A. 1901. Ueber Pseudomonotis Telleri und verwandte Arten der unteren Trias. Jahrbuch der k.k. Geologischen Reichsanstalt, 50:559–592.

Blakey, R. 2012. Global Paleogeography. http://www2.nau.edu/rcb7/globaltext2.html (accessed May 2012).

Bottjer, D. J., J. K. Schubert, and M. L. Droser. 1996. Comparative evolutionary palaeoecology: Assessing the changing ecology of the past. Geological Society, London, Special Publications, 102:1–13.

Boyer, D. L., D. J. Bottjer, and M. L. Droser. 2004. Ecological signature of Lower Triassic shell beds of the western United States. Palaios, 19:372–380.

Brayard, A., G. Escarguel, H. Bucher, C. Monnet, T. Brühwiler, N. Goudemand, T. Galfetti, and J. Guex. 2009. Good genes and good luck: Ammonoid diversity and the end–Permian mass extinction. Science, 325:1118–1121.

Broglio Loriga, C., D. Masetti, and C. Neri. 1983. La Formazione di Werfen (Scitico) delle Dolomiti occidentali: Sedimentologia e biostratigrafia. Rivista Italiana di Paleontologia e Stratigrafia, 58:501–598.

Broglio Loriga, C., F. Goczan, J. Haas, K. Lenner, C. Neri, A. Oravecz Sheffer, R. Posenato, I. Szabo, and A. Toth Makk. 1990. The Lower Triassic sequences of the Dolomites (Italy) and Transdanubian Mid-Mountains (Hungary) and their correlation. Memorie di Scienze Geologiche, Università di Padova, 42:41–103.

Broglio loriga, C. and S. Mirabella. 1986. II genere *Eumorphotis* Bittner 1901 nella biostratigrafia dello Scitico, Formazione di Werfen (Dolomiti). Memorie di Scienze Geologiche, 38:245–281.

Bronn, H. G. 1849. Index Palaeontologicus oder Übersicht der bis jetzt bekannten fossilen Organismen. Zweite Abtheilung. Enumerator palaeontologicus: Systematische Zusammenstellung und geologische Entwickelungs-Gesetze der organischen Reiche. Schweizerbart, Stuttgart, 776 p.

Bruguière J. G. 1797. Tableau Encyclopédique et Méthodique des trois Règnes de la Nature: Vers, coquilles, mollusques et polypes divers.

Campbell, K. S. W. 1965. Australian Permian terebratuloids. Bureau of Mineral Resources Geology and Geophysics Bulletin, 68:3–146.

Catullo, T. A. 1846. Memoria geognostico–paleozoica sulle Alpi Venete. Memorie della Società Italiana delle scienze residente in Modena, 24:1–158.

Chavan, A. 1954. Les Pleurophorus et genres voisins. Cahier Géologiques Seyssel, 22:200.

Chen, Z. Q., K. Kaiho, and A. D. George. 2005. Early Triassic recovery of the brachiopod faunas from the end-Permian mass extinction: A global review. Palaeogeography Palaeoclimatology Palaeoecology, 224:270–290.

Ciriacks, K. W. 1963. Permian and Eotriassic bivalves of the middle Rockies. Bulletin of the American Museum of Natural History, 125:1–100.

Clapham, M. E. and J. L. Payne. 2011. Acidification, anoxia, and extinction: A multiple logistic regression analysis of extinction selectivity during the Middle and Late Permian. Geology, 39:1059–1062.

Clark D. L. and T. R. Carr. 1984. Conodont biofacies and biostratigraphic schemes in western North America: A model. Geological Society of America Special Paper, 196:1–9.

Cossmann, M. 1906–1912. Essais de Paléoconchologie comparée. Livraison: 7(1906), 261 p.; 8(1909), 348 p.; 9(1912), 215 p. The author and Rudeval, Paris.

Cox, L. R. 1960. Thoughts on the classification of the Gastropoda. Proceedings of the Malacological Society of London, 33:239–261.

Cox, L. R., N. D. Newell, D. W. Boyd, C. C. Branson, R. Casey, A. Chavan, A. H. Coogan, C. Dechaseux, C. A. Fleming, F. Haas, L. G. Hertlein, E. G. Kauffman, A. Myra Keen, A. La Rocque, A. L. Mc Alaster, R. C. Moore, C. P. Nuttall, B. F. Perkins, H. S. Puri, L. A. Smith, T. Soot-Ryen, H. B. Stenzel, E. R. Trueman, R. D. Turner, and J. Weir. 1969. Bivalvia. *In* Moore, R. C. (ed.), Treatise on Invertebrate Paleontology. Part N. Mollusca 6. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas.

Cranford, P. J. and J. Grant. 1990. Particle clearance and adsorption of phytoplankton and detritus by the sea scallop Placopecten magellanicus (Gmelin). Journal of Experimental Marine Biology and Ecology, 137:105–121.

Cuvier, G. 1797–1798. Tableau élémentaire de l'histoire naturelle des animaux. Paris Baudouin, 710 p.

Dagys, A. S. 1965. Triasovye brakhiopody Sibiri [Triassic brachiopods of Siberia]. Nauka, Moskva, 187 p. (In Russian)

Dall, W. H. 1889. On the hinge of pelecypods and its development with an attempt toward a better subdivision of the group. American Journal of Science, 38:445–462.

Diener, C. 1923. Lamellibranchiata triadica. *In* C. Diener (ed.), Fossilium catalogus I: Animalia. Pars 19, 257 S., Berlin (W. Junk).

Duméril, A. M. C. 1806. Zoologie analytique ou méthode naturelle de classification des animaux. Allais, Paris, xxiv, 364 p.

Ekdale A. A. and T. R. Mason. 1988. Characteristic trace-fossil associations in oxygen-poor sedimentary environments. Geology, 16:720–723.

Erwin, D. H. 2001. Lessons from the past: Biotic recoveries from mass extinctions. Proceedings of the National Academy of Sciences of the United States of America, 98:5399–5403.

Frech, F. 1891. Die devonischen Aviculiden Deutschlands, ein Beitrag zur Systematik und Stammesgeschichte der Zweischaler. Abhandlungen zur Geologischen Spezialkarte von Preuen und den Thüringischen Staaten, 9:1–253.

FÜRSICH, F. T. 1984. Palaeoecology of boreal invertebrate faunas from the Upper Jurassic of Central East Greenland. Palaeogeography, Palaeoclimatology, Palaeoecology, 48:309–364.

FÜRSICH, F. T. 1994. Palaeoecology and evolution of Mesozoic salinity-controlled benthic macroinvertebrate associations. Lethaia, 26:327–346.

GALFETTI, T., H. BUCHER, M. OVTCHAROVA, U. SCHALTEGGER, A. BRAYARD, T. BRÜHWILER, N. GOUDEMAND, H. WEISSERT, P.A. HOCHULI, C. CORDEY, AND K. GUODUN, 2007. Timing of the Early Triassic carbon cycle perturbations inferred from new U–Pb ages and ammonoid biochronozones. Earth Planetary and Science Letters, 258:593–604.

GIEBEL, C. 1855. Kritisches über die Myophorien des Muschelkalkes. Zeitschrift für die gesamten Naturwissenschaften, 5:34–36.

GIRTY, G. H. 1927. Descriptions of new species of Carboniferous and Triassic fossils. *In* G. R. Mansfield, (ed.), Geography Geology and Mineral Resources of Part of Southeastern Idaho with Descriptions of Carboniferous and Triassic Fossils by G. H. Girty. U.S. Geological Survey Professional Paper 152, 453 p.

GEYER, G., M. HAUTMANN, H. HAGDORN, W. OCKERT, AND M. STRENG, 2005. Well-preserved mollusks from the lower Keuper (Ladinian) of Hohenlohe (Southwest Germany). Paläontologische Zeitschrift, 79:429–460.

GORYANSKY, V. YU, AND L. E. POPOV. 1985. Morphology, systematic position and origin of the inarticulate brachiopods with calcareous shells. Paleontologicheskii Zhurnal, 1985:3–14.

GRAY, J. E. 1847. A list of the genera of Recent Mollusca, their synonyms and types. Proceedings of the Zoological Society of London, 15:129–219.

GROBBEN, C. 1894. Zur Kenntnis der Morphologie, der Verwandtschaftsverhältnisse und des Systems der Mollusken. Sitzungsberichte der Akademie der Wissenschaften Wien, 103:61–86.

HALLAM, A. 1991. Why was there a delayed radiation after the end–Palaeozoic extinctions? Historical Biology, 5:257–262.

HALLAM, A. AND P. B. WIGNALL, 1997. Mass Extinctions and Their Aftermath. Oxford University Press, 328 p.

HAMMER, Ø, D. A. T. HARPER, AND P. D. RYAN, 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica, 4, 9 p. http://palaeo–electronica.org/2001_1/past/issue1_01.htm

HAUER, F. VON. 1850. Ueber die von Herrn Bergrath W. Fuchs in den Venetianer Alpen gesammelten Fossilien. Denkschriften der Akademie der Wissenschaften, Mathematisch–Naturwissenschaftliche Klasse, 2:109–126.

HAUTMANN, M. 2004. Early Mesozoic evolution of alivincular bivalve ligaments and its implications for the timing of the "Mesozoic marine revolution". Lethaia, 37:165–172.

HAUTMANN, M., H. BUCHER, T. BRÜHWILER, N. GOUDEMAND, A. KAIM, AND A. NÜTZEL. 2011. An unusually diverse mollusc fauna from the earliest Triassic of South China and its implications for benthic recovery after the end–Permian biotic crisis. Geobios, 44:71–85.

HAUTMANN, M. AND A. NÜTZEL. 2005. First record of a heterodont bivalve (Mollusca) from the Early Triassic: Palaeoecological significance and implications for the 'Lazarus problem'. Palaeontology, 48:1131–1138.

HAUTMANN, M., A. B. SMITH, A. J. MCGOWAN, AND H. BUCHER. 2013. Bivalves from the Olenekian (Early Triassic) of southwestern Utah: Systematics and evolutionary significance. Journal of Systematic Palaeontology, 11:263–293.

HERTWIG, C. W. T. R. 1895. Lehrbuch der Zoologie (third edition). Fischer, Jena, 599 p.

HOFMANN, R., N. GOUDEMAND, M. WASMER, H. BUCHER, AND M. HAUTMANN. 2011. New trace fossil evidence for an early recovery signal in the aftermath of the end-Permian mass extinction. Palaeogeography, Palaeoclimatology, Palaeoecology, 310:216–226.

HOFMANN, R., M. HAUTMANN, M. WASMER, AND H. BUCHER. 2013. Palaeoecology of the Virgin Formation (Utah, U.S.A.) and its implications for the Early Triassic recovery. Acta Palaeontologica Polonica, 58:49–173.

HOOVER, P. R. 1979. Early Triassic terebratulid brachiopods from the western interior of the United States. U.S. Geological Survey Professional Paper, 1057:1–21.

JABLONSKI, D., J. J. SEPKOSKI, D. J. BOTTJER, AND P. M. SHEEHAN. 1983. Onshore–offshore patterns in the evolution of Phanerozoic shelf communities. Science, 222:1123–1125.

JACCARD, P. 1901. "Étude comparative de la distribution florale dans une portion des Alpes et des Jura", Bulletin de la Société Vaudoise des Sciences Naturelles, 37:547–579.

KAIM, A. 2009. Gastropods, p. 141–156. *In* Y. SHIGETA, Y. D. ZAKHAROV, H. MAEDA, and A. M. POPOV (eds.), The Lower Triassic System in the Abrek Bay Area, South Primorye, Russia. National Museum of Nature and Science Monographs, 38.

KAIM, A. AND A. NÜTZEL. 2011. Dead bellerophontids walking—the short Mesozoic history of the Bellerophontoidea (Gastropoda). Palaeogeography, Palaeoclimatology, Palaeoecology, 308:190–199.

KAIM, A., A. NÜTZEL, H. BUCHER, T. BRÜHWILER, AND N. GOUDEMAND. 2010. Early Triassic (late Griesbachian) gastropods from South China (Shanggan, Guangxi). Swiss Journal of Geosciences, 103:121–128.

KAUFFMAN, E. G. AND P. J. HARRIES. 1996 The importance of crisis progenitors in recovery from mass extinction, p. 15–39. *In* M. B. Hart (ed.), Biotic Recovery from Mass Extinction Events. Geological Society, London, Special Publications, 102.

KIPARISOVA, L. D. 1938. Nizhnetriasovye plastinchatozhabernye Ussurijskogo kraya. Trudy Geologicheskogo Instituta, 7:197–311. (In Russian)

KIPARISOVA, L. D. AND A. N. KRISHTOFOVICH 1954. Polevoj atlas kharakternykh kompleksov fauny i fiery triasovykh otlozhenij primorskogo kraya [Field atlas of typical complexes offauna and flora of Triassic deposits in Primorye region]. Gosgeoltekhizdat, Moscow, 127 p. (In Russian)

KITTL, E. 1894. Die Gastropoden der Schichten von St. Cassian der südalpinen Trias. 3. Theil. Annalen des kaiserlich–koniglichen Naturhistorischen Hofmuseums, 9:143–275.

KITTL, E. 1904. Geologie der Umgebung von Sarajevo. Jahrbuch der Geologischen Reichsanstalt (for 1903), 53:707–738.

KRYSTYN, L., L. RICHOZ, S. BAUD, AND R. J. TWITCHETT. 2003. A unique Permian–Triassic boundary section from the Neotethyan Hawasina Basin, Central Oman Mountains. Palaeogeography, Palaeoclimatology, Palaeoecology, 191:329–344.

KUMAGAE, T. AND K. NAKAZAWA. 2009. Bivalves, p. 156–173. *In* Y. Shigeta, Y. D. Zakharov, H. Maeda, and A. M. Popov (eds.), The Lower Triassic System in the Abrek Bay Area, South Primorye, Russia. National Museum of Nature and Science Monographs, 38.

KUMMEL, B. 1954. Triassic stratigraphy of Southeastern Idaho and adjacent areas. Geological Survey Professional Paper, 254:165–194.

KUMMEL, B. 1957 Paleoecology of Lower Triassic formations of southeastern Idaho and adjacent areas. Memoirs of the Geological Society of America, 67:437–468.

LAMARCK, J. B. 1819. Histoire naturelle des Animaux sans vertèbres. Classe onzième. Les Conchifères, 6:1–258.

LINNAEUS, C. 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tomus I. Editio Decima. Laurentius Salvius, Stockholm, 824 p.

MARWICK, J. 1953. Divisions and faunas of the Hokonui system (Triassic and Jurassic). New Zealand Geological Survey, Paleontological Bulletin, 21:1–141.

MANSFIELD, G. R. 1927. Geography, Geology, and Mineral Resources of Part of Southeastern Idaho. U.S. Geological Survey Professional Paper 152, 453 p.

MATA, S. A. AND D. J. BOTTJER. 2011. Origin of Lower Triassic microbialites in mixed carbonate-siliciclastic successions: ichnology, applied stratigraphy, and the end–Permian mass extinction. Palaeogeography, Palaeoclimatology, Palaeoecology, 300:158–178.

MAUGHAN, E. K. 1979. Petroleum source rock evaluation of the Permian Park City Group in the northeastern Great Basin, Utah, Nevada, and Idaho, p. 523–530. *In* G. W. Newman and H. D. Goode (eds.), Basin and Range Symposium. Rocky Mountain Association of Geologists and Utah Geological Association.

MCCARTHY P. T. AND D. M. MILLER. 2002. Geologic map of the Terrace Mountain East quadrangle, Box Elder County, Utah. Utah Geological Survey Miscellaneous Publication 02, 13 p.

MCCOY, F. 1852. A Synopsis of the Classification of the British Palaeozoic Rocks [By the Rev. Adam Sedgwick] with a Systematic Description of the British Palaeozoic Fossils in the Geological Museum of the University of Cambridge [by Frederick McCoy] with Figures of the New and Imperfectly Known Species. Parker and Son, London, 661 p.

MCROBERTS, C. A. AND C. R. NEWTON. 1995. Selective extinction among end-Triassic European bivalves. Geology, 23:102–104.

MEEK, F. B. AND F. V. HAYDEN, 1864. Palaeontology of the Upper Missouri. Smithsonian Contributions to Knowledge, 14:1–135.

MEEK, F. B. 1877. Part I Palaeontology, p. 1–197. *In* C. KING (ed.), Annual Report to the Secretary of War on the U.S. Geological Exploration of the Fortieth Parallel 4. Government Printing Office, Washington.

MENKE, C. T. 1828. Synopsis methodica Molluscorum generum omnium et specie rum earum, quae in Museo Menkeano Adservantur. Pyrmonti, 91 p.

MILLER, S. A. 1877. The American Paleozoic fossils: A catalogue of the genera and species. Published by the author, Cincinnati, 334 p.

MILLER, A. I. 1988. Spatio–temporal transitions in Paleozoic bivalvia: An analysis of North American fossil assemblages. Historical Biology, 1:251–273.

MORISITA, M. 1959: Measuring of interspecific association and similarity between communities. Memoires of the Faculty of Science, Kyushu University, Series E. Biology, 3:65–80.

MUNDIL, R., K. R. LUDWIG, I. METCALFE, P. R. RENNE. 2004. Age and timing of the Permian mass extinctions: U/Pb dating of closed system zircons. Science, 305:1760–1763.

MULLER, S. W. AND H. G. FERGUSON. 1939. Mesozoic stratigraphy of the Hawthorne and Tonopah quadrangles, Nevada. Geological Society of America Bulletin, 50:1573–1624.

MÜNSTER, G. GRAF ZU 1841. Beiträge zur Petrefacten–Kunde. IV. Beschreibung und Abbildung der in den Kalkmergelschichten von St. Cassian gefundenen Versteinerungen. Buchner'sche Buchhandlung, 152 p.

MUSTER, H. 1995. Taxonomie und Paläobiogeographie der Bakevelliidae (Bivalvia). Beringeria, 14:1–161.

NAKAZAWA, K. 1977. On *Claraia* of Kashmir and Iran. Journal of the Palaeontological Society of India, 20:191–204.

NEWELL, N. D. 1938. Late Paleozoic pelecypods: Pectinacea. State Geological Survey of Kansas Publications, (for 1937), 10:1–123.

NEWELL, N. D. 1955. Permian pelecypods of east Greenland. Meddelelser om Grønland, 110:1–36.

NEWELL, N. D. 1965. Classification of the Bivalvia. American Museum Novitates, 2206:1–25.

NEWELL, N. D. 1969. Order Modiomorphoida Newell, new order, p. N393. *In* R. C. Moore (ed.), Treatise on Invertebrate Paleontology, Part N, Mollusca 6, Volume 1. Geological Society of America and University of Kansas Press, Boulder.

NEWELL, N. D. AND D. W. BOYD 1995. Pectinoid bivalves of the Permian–Triassic crisis. American Museum of Natural History Bulletin, 227:1–95.

NEWELL, N. D. AND D. W. BOYD 1999. A new Lower Triassic Permophorus from the Central Rocky Mountains. American Museum Novitates, 3263:1–5.

NEWELL, N. D. AND B. KUMMEL. 1942. Lower Eo-Triassic stratigraphy, western Wyoming and southeast Idaho. Geological Society of America Bulletin, 53: 937–995.

OVTCHAROVA, M., H. BUCHER, U. SCHALTEGGER, T. GALFETTI, A. A. BRAYARD, AND J. GUEX. 2006. New Early to Middle Triassic U–Pb ages from South China: Calibration with ammonoid biochronozones and implications for the timing of the Triassic biotic recovery. Earth and Planetary Science Letters, 243:463–475.

PAULL, R. K. AND R. A. PAULL. 1994. Shallow marine sedimentary facies in the earliest Triassic (Griesbachian) Cordilleran Miogeocline, U.S.A. Sedimentary Geology, 93:181–191.

PRUSS, S. B. AND D. J. BOTTJER. 2004. Early Triassic trace fossils of the western United States and their implications for prolonged environmental stress from the end-Permian mass extinction. Palaios, 19:551–564.

RAUP, D. M. 1979. Size of the Permo-Triassic bottleneck and its evolutionary implications. Science, 206:217–218.

RODLAND D. L. AND D. J. BOTTJER. 2001. Biotic recovery from the end-Permian mass extinction: Behavior of the inarticulate brachiopod Lingula as a disaster taxon. Palaios, 16:95–101.

SAVRDA C. E. AND D. J. BOTTJER. 1986. Trace-fossil model for reconstruction of paleo-oxygenation in bottom waters. Geology, 14:3–6.

SCHAUROTH, K. VON. 1859. Kritisches Verzeichnis der Versteinerungen der Trias im Vicentinischen. Sitzungsberichte der Kaiserlichen Akademie derWissenschaftenWien, Mathematisch-Naturwissenschaftliche Classe, 34: 283–356.

SCHOLTEN, R., K. A. KEENMON, AND W. O. KUPSCH. 1955. Geology of the Lima region, southwestern Montana and adjacent Idaho. Bulletin of the Geologic Society of America, 66:345–404.

SCHUBERT, J. K. AND D. J. BOTTJER. 1995. Aftermath of the Permian–Triassic mass extinction event-paleoecology of Lower Triassic carbonates in the western U.S.A. Palaeogeography, Palaeoclimatology, Palaeoecology, 116: 1–39.

SCHULBERT, C. AND A. NÜTZEL. 2005. Facies of two important Early Triassic gastropod lagerstätten: implications for diversity patterns in the aftermath of the end-Permian mass extinction. Facies, 51:495–515.

SCOPOLI, J. A. 1777. Introdvctio ad historiam natvralem sis tens genera lapidvm, plantarvm, et animalivm hactenvs detecta, caracteribvs essentialibvs donata, in tribvs divisa, svbinde ad leges natvrae. Apvd Wolfgangvm Gerle, Prague, 506 p.

SEPKOSKI, J. J. 1988. Alpha, beta, or gamma—where does all the diversity go. Paleobiology, 14:221–234.

SHIGETA, YU. Y., D. ZAKHAROV, H. MAEDA, AND A. M. POPOV (eds.). 2009. The Lower Triassic System in the Abrek Bay Area, South Primorye, Russia. National Museum of Nature and Science Monographs, 38, 218 p.

SIMROTH, H. 1906. Mollusca, p. 85–89. *In* H. G. Bronn (ed.), Klassen und Ornungen des Tier–Reichs, 2nd Edition, Volume 3.

SPATH, L. F. 1930. The eotriassic invertebrate fauna of east Greenland. Meddelelser om Grønland, 83:1–90.

STIFEL, P. B. 1964. Geology of the Terrace and Hogup Mountains, Box Elder County, Utah. Ph.D. dissertation. University of Utah, Salt Lake City, 173 p.

STANLEY, M. S. 1972. Functional morphology and evolution of byssally attached bivalve mollusks. Journal of Paleontology, 46:165–212.

TWITCHETT, R. J. 2006. The palaeoclimatology, palaeoecology and palaeoenvironmental analysis of mass extinction events. Palaeogeography, Palaeoclimatology, Palaeoecology, 232:190–213.

TWITCHETT, R. J. AND C. G. BARRAS. 2004. Trace fossils in the aftermath of mass extinction events, p. 397–418. *In* D. McIlroy (ed.), The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis. Geological Society, London.

TWITCHETT, R. J. AND P. B. WIGNALL. 1996. Trace fossils and the aftermath of the Permo-Triassic mass extinction: Evidence from northern Italy. Palaeogeography, Palaeoclimatology, Palaeoecology, 124:137–151.

TWITCHETT, R. J., L. KRYSTYN, A. BAUD, J. R. WHEELEY, AND S. RICHOZ. 2004. Rapid marine recovery after the end-Permian mass-extinction event in the absence of marine anoxia. Geology, 32:805–808.

WAAGEN, W. 1883. Productus Limestone Fossils, Part IV, fas. 2. Salt Range Fossils, Palaeontologia Indica, Series 13, 1:391–546.

WAAGEN, W. 1895. Salt-Range fossils, Vol. 2, Fossils from the Ceratite Formation. Pisces–Ammonoidea (Cephalopoda). Memoirs of the Geological Survey of India, Palaeontologia Indica, 13:1–323.

WALLER, T. R. 1978. Morphology, morphoclines and a new classification of the Pteriomorphia (Mollusca: Bivalvia). Philosophical Transactions of the Royal Society of London, Ser. B, 284:345–365.

WARE, D., J. F. JENKS, M. HAUTMANN, AND H. BUCHER. 2011. Dienerian (Early Triassic) ammonoids from the Candelaria Hills (Nevada, U.S.A.) and their significance for palaeobiogeography and palaeoceanography. Swiss Journal of Geosciences, 104:161–181.

WASMER, M., M. HAUTMANN, E. HERMANN, D. WARE, G. ROOHI, K. UR–REHMAN, A. YASEEN, AND H. BUCHER. 2012. Olenekian (Early Triassic) bivalves from the Salt Range and Surghar Range, Pakistan. Palaeontology, 55:1043–1073.

WHITTAKER, R. H. 1972. Evolution and Measurement of Species Diversity. Taxon, 21:213–251.

WHITTAKER, R. H. 1975. Communities and Ecosystems. Macmillan, New York, xviii, 385 p.

WIGNALL, P. B. AND A. HALLAM. 1992. Anoxia as a cause of the Permian Triassic mass extinction-facies evidence from northern Italy and the western United States. Palaeogeography, Palaeoclimatology, Palaeoecology, 93:21–46.

WILLIAMS, A., S. J. CARLSON, C. H. BRUNTON, L. E. HOLMER, AND L. E. POPOV. 1996. A supra-ordinal classification of the Brachiopoda. Philosophical Transactions of the Royal Society, Biological Sciences, 35:1171–1193.

WITTENBURG, P. VON. 1908. Beiträge zur Kenntnis der Werfener Schichten Südtirols. Geologische und Paläontologische Abhandlungen, neue Folge, 8: 251–289.

YÜ, W. 1975. The Gastropod Fossils from the Qomolangma Feng Region. Science Press, Peking, 214 p. (In Chinese)

ZIETHEN, C. H. VON. 1830. Die Versteinerungen Württembergs. Verlag and Lithographie des Werkes Unsere Zeit, Stuttgart, 102 p.

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Chapter 4

Recovery of benthic marine communities from the end-Permian mass extinction at the low-latitudes of Eastern Panthalassa

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"They have no face, no place for ears
There's no clam eyes, to cry clam tears
No spinal cord, they must get bored
Might as well just put them out of misery"

from "Clams Have Feelings Too (Actually They Don't)" by NoFX
Album: Pump Up the Valuum
Epitaph (2000)

Recovery of benthic marine communities from the end-Permian mass extinction at the low-latitudes of Eastern Panthalassa

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Abstract: Based on quantitative community analysis using species level identifications, we track the restoration of benthic ecosystems after the end-Permian mass extinction throughout the Lower Triassic of the western US New data on the palaeoecology of the Thaynes Group and Sinbad Formation are provided, which fill a gap between the recently studied palaeoecology of the Griesbachian-Dienerian Dinwoody Formation and the Spathian Virgin Formation. In the Sinbad Formation and Thaynes Group, 17 species (12 genera) of bivalves, 7 species and genera of gastropods and 2 species and genera of brachiopods are recognized. The new bivalve genus *Confusionella* (Pteriidae) is described. A comprehensive review of the whole Lower Triassic succession of benthic ecosystems of the western US indicates that mid and inner shelf environments show incipient recovery signals around the Griesbachian-Dienerian transition, during the Smithian and, most profound, during the early Spathian. Ecological data from youngest strata of the Dinwoody Formation as well as stratigraphic ranges of species suggest that the late Dienerian was likely a time interval of environmental stress for benthic ecosystems. Despite some evidence for short-term environmental disturbances (e.g. shift of dominant taxa, transient drop in alpha diversity) during the Smithian-Spathian transition, benthic ecosystems did not show any notable taxonomic turnover at that time, in contrast to the major crisis that affected ammonoids and conodonts. Whereas alpha diversity of benthic communities generally increased throughout the Early Triassic, beta diversity remained low, which reflect a persistently wide environmental range of benthic species. This observation is in accordance with a recently proposed model that predicts a time lag between increasing within-habitat diversity (alpha-diversity) and the onset of taxonomic differentiation between habitats (beta-diversity) during biotic recoveries from mass extinction events. The observation that beta-diversity had not significantly increased during the Early Triassic might also provide an explanation for the comparably sluggish increase of benthic diversity during that time, which has previously been attributed to persistent environmental stress. **Key words:** recovery • benthic ecosystems • Thaynes • Sinbad • palaeoecology • diversity

RECENT studies (e.g. Krystyn et al. 2003, Brayard et al. 2009, Hautmann et al. 2011, 2013; Hofmann et al. 2011, 2013a) provided evidence that the recovery from the end-Permian mass extinction was more volatile than traditionally portrayed (e.g. Hallam 1991; Schubert and Bottjer 1995; Twitchett and Wignall, 1996), suggesting that ecosystems suffered from several short-term environmental perturbations during the Early Triassic rather than from long-lasting environmental stress. Furthermore, it has been suggested intrinsic aspects (Schubert and Bottjer 1995), most notably reduced interspecific competition had an important impact on the pace of recovery (Hofmann et al. 2013a,b). The Lower Triassic of the western US provides one of the best worldwide records of Early Triassic benthic ecosystems, which facilitates tracing benthic recovery from the end-Permian mass extinction through different time slices, represented by comparable sets of habitats from the same palaeogeographic region. In previous papers (Hautmann et al. 2013; Hofmann et al. 2013a,b) we re-evaluated the taxonomy and palaeoecology of the Griesbachian-Dienerian and the Spathian faunas from the western US. Here, we add data on Smithian–early Spathian benthic palaeocommunities of the same region. Together, these data allow us to draw a complete picture of the recovery of benthic marine ecosystems at the eastern Panthalassa margin. We thereby address the question of intrinsic and extrinsic controls of recovery and test a previously proposed model (Hofmann et al. 2013b) on changes in diversity partitioning during rediversification after major diversity depletions.

GEOLOGICAL AND STRATIGRAPHICAL SETTING OF THE THAYNES GROUP AND THE SINBAD FORMATION

The Thaynes Group is today exposed over an area stretching from southern Wyoming, eastern and central Idaho, Utah, and northeastern Nevada. It represents a relatively shallow epicontinental marine embayment of the eastern Panthalassa Ocean (Fig. 1). The Thaynes Group reaches a thickness of about 1000 m in its depotcentre (western Utah and southeastern Idaho, own observation HB) and pinches out towards the south, east, and west. The Thaynes Group records generally epicontinental open marine deposits composed of alternating shale, marl, siltstone and limestone (Fig. 2, 3A). These strata result from a major transgression reaching its maximum extent during the late Smithian (e.g. Collinson and Hasenmueller 1978; Carr

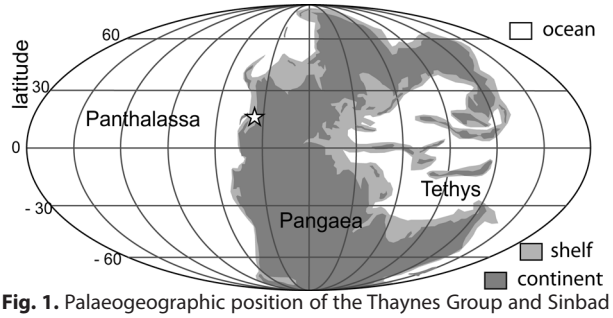

Fig. 1. Palaeogeographic position of the Thaynes Group and Sinbad Formation during the Early Triassic (map after Blakey 2012).

TABLE 1. Geographic information on the logged sections.

Code	Section	Geographic Information	GPS coordinates (WGS 84)
DH-1	Disappointment Hills 1	Confusion Range, Utah	39°24′42.42″N, 113°41′22.23″W
DH-3	Disappointment Hills 3	Confusion Range, Utah	39°24′52.20″N, 113°40′50.00″W
CP	Cowboy Pass	Confusion Range, Utah	39°20′23.55″N, 113°41′43.79″W
DV	Dog Valley	Pahvant Range, Utah	38°40′22.80″N, 112°31′18.20″W
MV	Minersville	Mineral Mountains, Utah	38°13′43.00″N, 112°53′17.40″W
SR	Sand Rafael Swell	central Emery County, Utah	38°59′49.29″N, 110°40′44.26″W
TO	Torrey	west Wayne County, Utah	38°16′20.00″N, 111°23′05.30″W

and Paull 1983; Paull and Paull 1993). Lucas et al. (2007) proposed raising the Thaynes Formation to Group status and also included shallow and marginal marine deposits of the Sinbad and Virgin Formations (Fig. 2). However, as already noted by Hofmann et al. (2013b), the typical lithologies of both Formations are exclusively developed in southern Utah where they are easily recognized within the Moenkopi Group (as proposed by Poborsky 1954, and endorsed by Lucas et al. 2007). To retain nomenclatural consistency with respect to the Sinbad and the Virgin Formation, we follow Lucas et al. (2007) and refer to the Thaynes Group for clearly marine Lower Triassic strata of the Confusion Range and we extend its use into the Pahvant Range and Mineral Mountains. The Sinbad Formation of southern Utah is mainly composed of bioclastic limestones, calcareous sandstones and dolomites deposited in inner shelf and marginal marine settings. It roughly delineates the maximum coastal onlap of marine strata during the Smithian in southern Utah.

Smithian outcrops in Utah generally contain abundant fossils, but no detailed regional biostratigraphic zonation has been proposed for this substage. All previous dates obtained from macrofossils are based on ammonoids with the twofold subdivision suggested by Kummel and Steele (1962): the *Meekoceras gracilitatis* Zone and the *Anasibirites kingianus* Zone, in the ascending order. However, Brayard et al. (2009) and Stephen et al. (2010) recently demonstrated that these zones represent only the middle and late Smithian and can be subdivided into more precise different subzones and beds. Based on new ammonoid faunas, older Smithian deposits also occur within some restricted areas. Therefore, we use a new ammonoid biozonation (Fig. 3B; Brayard et al. 2011, Brayard et al. 2013a).

FIELD LOCALITIES AND METHODS

Fieldwork was conducted in October 2009 (by RH, AB, KB, JJ) in the area of the Pahvant Range and the Confusion Range. In June 2011, we (RH, MH, AB, JJ, KB, EV, NO) investigated sections in the Mineral Mountains, the San Rafael Swell and the Torrey area (see Table 1 for detailed geographic information). Bed by bed logging was carried out at five sections of the Thaynes Group and two sections of the Sinbad Formation. Fossils were collected from discrete limestone and calcareous sandstone beds by mechanically decomposing large blocks and quantitative sampling for identifiable specimens. In shale intervals, fossils were representatively sampled by collecting from float material. If necessary, standard invertebrate preparation techniques were carried out to facilitate systematic examination. Beds showing evidence of reworking (e.g. notable size-sorting, gradation, strong fossil abrasion) were not included in the analysis. Sampling of each bed was conducted until more than 100 specimens were obtained or until additional collecting did not result in finding new taxa. However, some outcrop conditions did not allow for comprehensive sampling.

Sedimentological analysis was mainly based on macroscopic criteria in the field. Taxa recognized herein include bivalves, gastropods and brachiopods. Abundance data of the samples were analysed with PAST version 2.17c (Hammer et al. 2001) using unweighted paired group Q-mode cluster analysis. The Morisita index of similarity (Morisita 1959) was used as distance measure which is has been recommended for palaeoecological data (Hammer and Harper 2006). This procedure has been applied successfully in Hofmann et al. (2013a) and

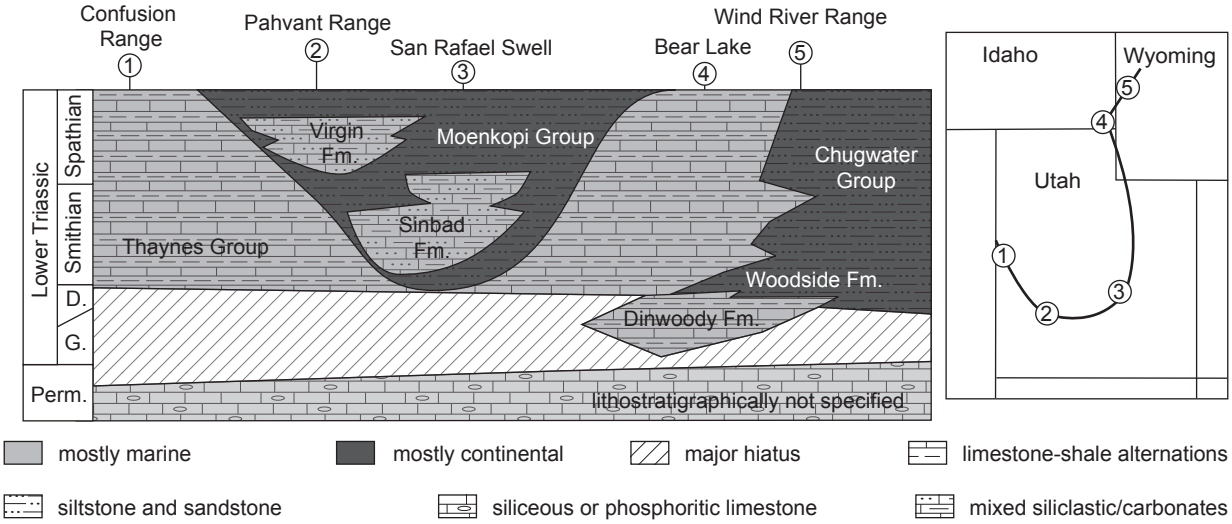

FIG. 2. Principle lithostratigraphic relationships of upper Permian to lower Spathian rocks of Utah, Wyoming and Idaho. Several Formations that are recognized in the marginal-marine to continental siliclastic facies of the Moenkopi group were omitted to enhance readability. The scheme rests on visualizations and data provided by Blakey (1974), Clark and Carr (1984), Cavaroc and Forles (1991) as well as own observations. Vertical dimensions are not to scale with actual time or thickness. D. – Dienerian, G. – Griesbachian, Perm. – Permian, Fm. – Formation.

Hofmann et al. (2013b) to detect recurrent assemblages of taxa in very similar data sets. All subclusters and respective samples with a Morisita-similarity approximately higher than 0.4 were pooled into associations (e.g. Aberhan 1992). These new species-abundance data were than used to compute ranked species abundance, trophic nuclei, ecological pie-charts and rarefaction analysis. The trophic nucleus is represented by those species that contribute to at least 80 percent of total specimen number per association (Neyman 1967). Taxonomic evenness of samples is given as dominance index D as obtained from PAST (Hammer et al. 2001).

Diversity partitioning is analysed at the within-community (alpha-diversity) and Sepkoski (1988) defined alpha-diversity as the species richness in a single localitity or sample. Whittaker (1972) understood alpha-diversity as the number of species in a given area or community. The first one, sample richness (alpha-diversity sensu Sepkoski 1988), is herein referred to as species richness (of a sample). The cluster algorithm was used to reconstruct communities based on recurrent associations of species. Accordingly, we use alpha-diversity to account for the bulk diversity of merged samples that constitute an association as an approximation of a palaeocommunity. A single bed would represent an incomplete sample of such a palaeocommunity and, thus, would highly underestimate the alpha-diversity. Beta-diversity is a measure for the taxonomic differentiation between-community (beta-diversity) level, following the original concept of Whittaker (1972, 1977). Some subsequent studies used sample diversity rather than community diversity as 'alpha-diversity'(e.g., Bambach 1977; Sepkoski 1988), which has the advantage that it does not depend from the somewhat

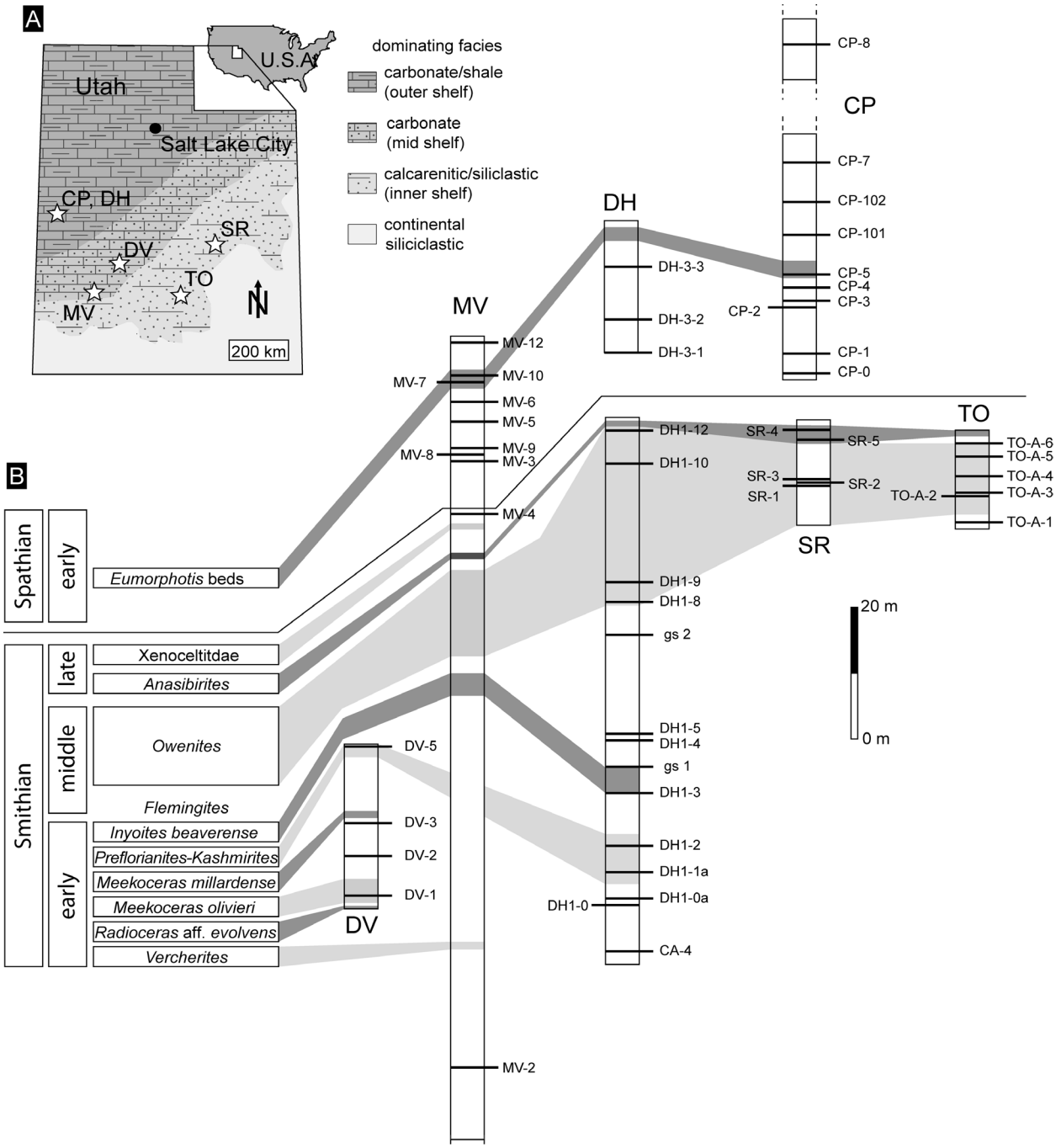

FIG. 3. A, Map of the studied sections and their approximate palaoegeographic relationships as indicated by predominating facies types (CP – Cowboy Pass, DH – Disappointment Hills, MV – Mineral Mountains/Minersville, DV – Dog Valley, TO – Torrey, SR – San Rafael Swell). B, Stratigraphic correlation of the investigated sections showing the position of the sampled intervals.

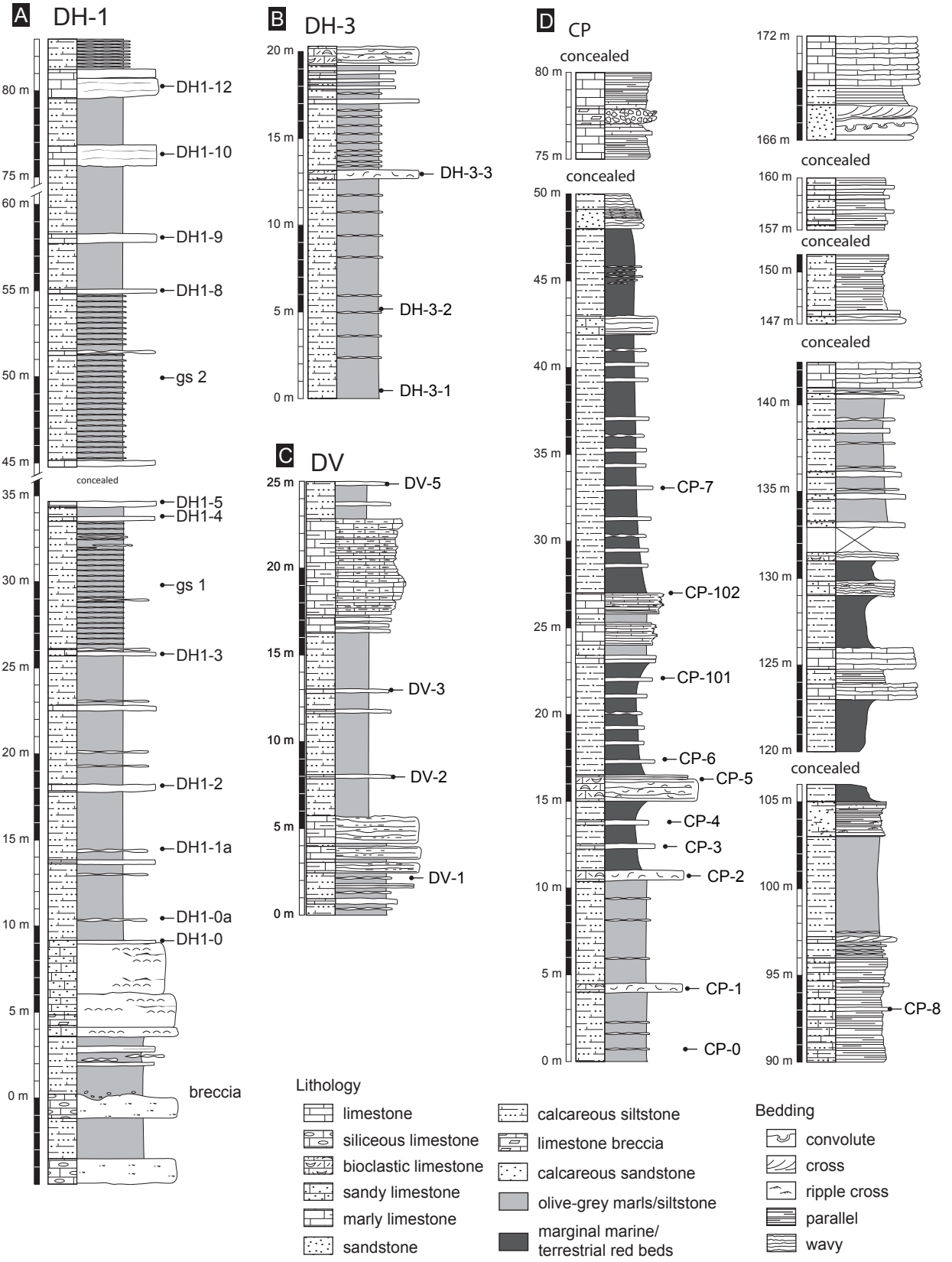

FIG. 4. Sections of the Thaynes Group. A, Disappointment Hills 1. B, Disappointment Hills 2. C, Dog Valley. D, Cowboy Pass. Map of the studied sections and their approximate palaoegeographic relationships as indicated by predominating facies types (CP – Cowboy Pass, DH – Disappointment Hills, MV – Mineral Mountains/Minersville, DV – Dog Valley, TO – Torrey, SR – San Rafael Swell). B, Stratigraphic correlation of the investigated sections showing the position of the sampled intervals.

subjective identification of recurrent assemblages and (probably more important) that it is much less time consuming. However, sample diversity is also subjective in the sence that it represents a random fraction from the bulk of palaeontologically identifiable organsims in the palaeocommunity/association, depending from the local conditions at the given sampling point. Additionally, sample or point diversity does not represent a natural ecological entity, as the community does. We therefore prefer using alpha-diversity in the original sence, and we minimalize the subjective aspect of palaeocommunity-identification by combining cluster analyses of palaeontological samples with sedimentological data for habitat discrimination. However, sample diversity is additionally discussed in the analyses of temporal and spatial trends.

Our basic measure of alpha-diversity is species richness, whereas beta-diversity (between associations/habitat diversity) is measured by the mean minimum beta-diversity approach proposed by Hofmann et al. (2013a). Appendix VI-D and V-C includes data sheets showing the full lists of species occurrences, associations.

AGE AND SEDIMENTARY ENVIRONMENTS OF THE INVESTIGATED SECTIONS

Confusion Range. The sampled part of the Disappointment Hills sections includes strata of the Smithian (DH-1, Fig. 4A) and the lowermost Spathian (DH-3, Fig. 4B). Some fossil specimens included in the systematic analysis come from a sampling point called DH-2B (base of section DH-2). This interval is poorly exposed but ammonoids suggest an early to middle Smithian age. The base of the section is composed of cherty limestones

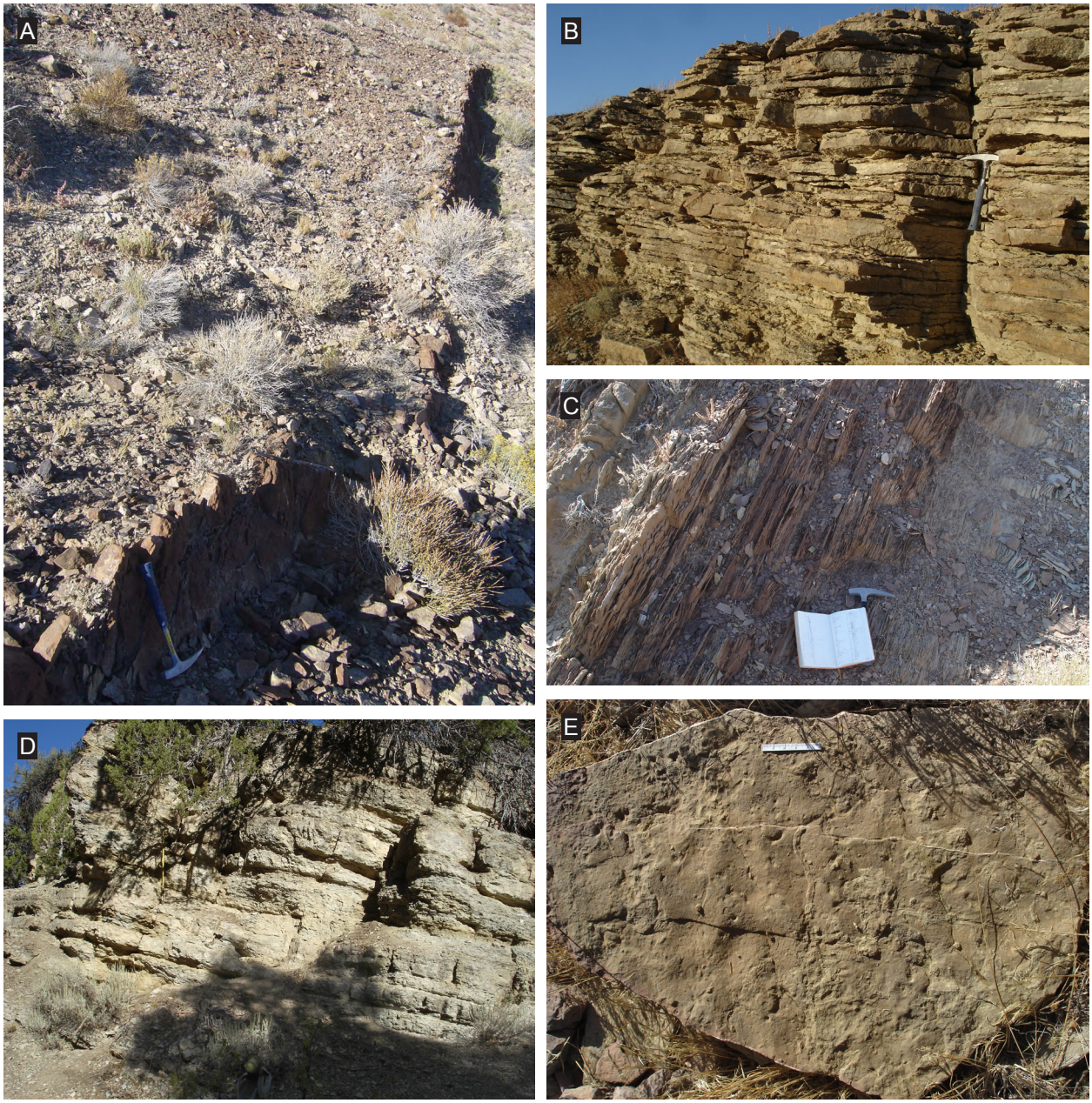

FIG. 5. Field photographs of the Thaynes Group. A, Claystone and siltstone intercalated with thin limestone beds of DH-1. Hammer for scale represents 35 cm. B, Bioclastic grainstones of the '*Eumorphotis*–beds'. Top of section DH-3. Hammer for scale represents 35 cm. C, Overturned, thinly bedded to laminated siltstones and claystones intercalated between thin bioclastic limestone around the Smithian Spathian transition of CP section. Fieldbook for scale represents 20 cm. D, Lower part of DV section exposing a marly limestone succession. The height of exposure is about 3 meters. E, Fine-grained sandstone of the upper part of section showing oscillation ripples in upper bedding plane view. Note the sparse bioturbation. Scale bar represents 5 cm.

of the Middle Permian Gerster Formation. The transition to the Triassic is complex. Discontinuous upper surfaces of limestone beds and the presence of breccias, conglomerates as well as some poorly exposed red beds suggest a complex history of episodes with emersion, erosion and non-deposition. The age of the massive calcarenites above the Permian hiatus is uncertain, but these beds may correspond to Lower Triassic strata. Above this interval, the section DH-1 is mainly composed of olive to brown shales and marls alternating with fossiliferous packstone and grainstone beds. Abundant ammonoids allow a precise correlation with Smithian ammonoid zones (Fig. 3).

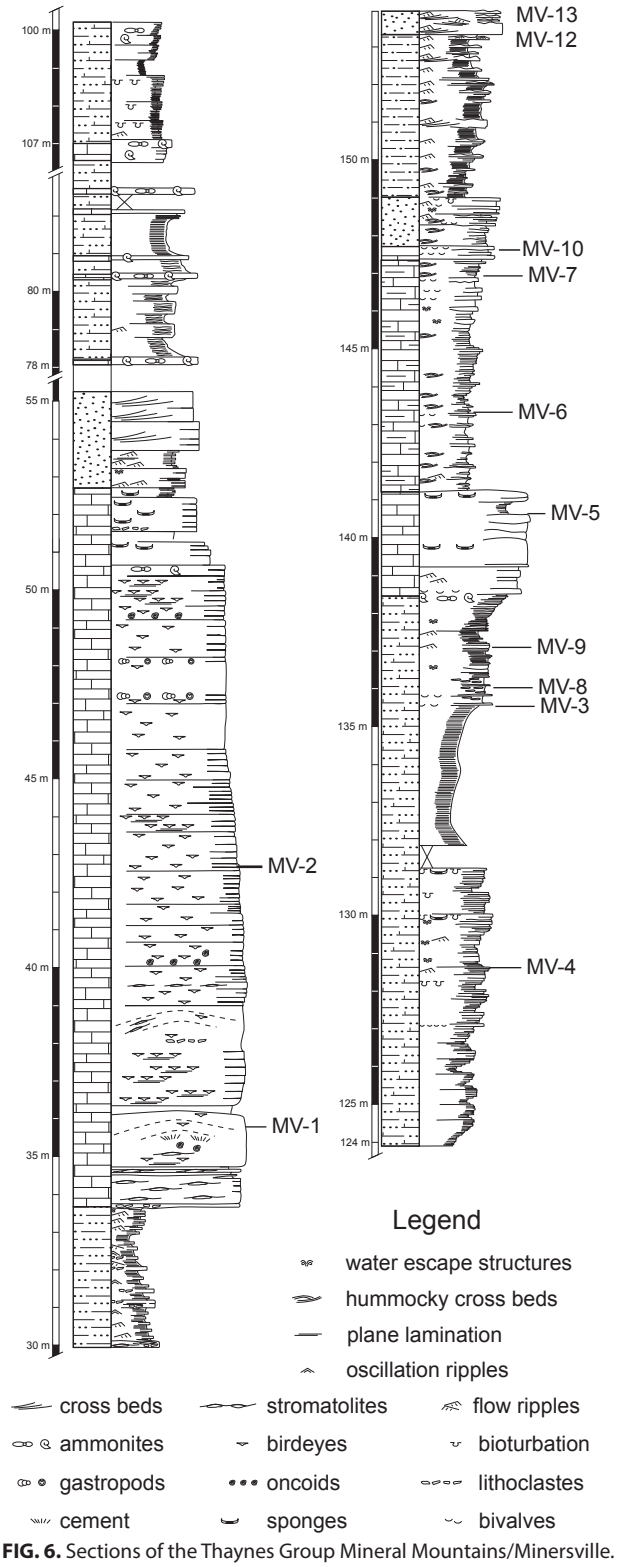

FIG. 6. Sections of the Thaynes Group Mineral Mountains/Minersville.

The shale intervals (Fig.5A) were deposited out of suspension in quiet waters of the outer shelf region. The pack- and grainstone associated facies is indicative of storm-induced conditions deposited around the mid/outer shelf transition as evidence for active wave reworking (e.g. cross bedding, ripple cross lamination) is absent. The overall presence of ammonoids in the section DH-1 indicates an open marine setting. A covered shaly interval with an estimated thickness of about 50 metre separates sections DH-1 and DH-3. The latter section is mainly composed of laminated greenish shales with thin mudstone beds. The section is topped by a series of medium bedded bioclastic limestone beds (Fig. 5B) with large bivalves of the genus Eumorphotis, which are frequently observed in life position. These beds are widespread in the study area and mark the transition to the Spathian as they characteristically occur between the youngest Smithian and the oldest Spathian (*Bajarunia confusionensis* beds, Guex et al. 2010) ammonoid zones (Fig. 3). They typically consist of bioclastic grain- and rudstones and are intercalated with thin marlstones. These beds are poorly sorted and show no evidence of gradation. We suggest that they represent proximal storm deposits which were colonized by large epifaunal bivalves during quiet phases. Accordingly, they most likely represent deposits of the middle shelf, between the mean fair weather- and the storm wave base. The same type of deposits are also recorded in the section at Cowboy Pass section (CP; Fig. 4D) and is herein used as a marker that allows for a continuous correlation of the Thaynes Group throughout the Confusion Range. At Cowboy Pass, the ensuing interval is characterized by red and purple siltstones and claystones, which are interbedded with some thin beds of pack- and grainstone (Fig. 5C). Some levels that exhibit ripple-cross laminated fine-grained sandstones showing some mud-drapes, suggest deposition in marginal marine and probably tidally influenced settings. The absence of stenohaline organisms such as crinoids and brachiopods, which both became abundant in Spathian deposits of the western US (Schubert and Bottjer 1995; Hofmann et al. 2013b) supports a restricted marginal marine setting. The first late Early Spathian-aged ammonoid faunas (Guex et al. 2010) and first abundant crinoidal debris suggesting an open marine setting are observed further up-section (~100 m above the *Eumorphotis* beds). These beds did not yield abundant benthic fauna. The section continues with outer shelf marls and shales, which are very poorly exposed and, thus, were not further investigated.

Pahvant Range. The base of the section at Dog Valley (DV, Fig. 4C) is composed of calcareous siltstones, and marly mudstones (Fig. 5D), which record early Smithian ammonoid faunas (Radioceras aff. evolvens beds). It is suggested that these strata record open marine conditions of a mid to outer shelf setting. The overlying interval is composed of shales and marls indicative of an outer shelf facies. Overlying the shales and marls is an interval of compact marly and sandy limestones with abundant bedding-plane horizontal bioturbation, and occasionally intercalated beds showing oscillation ripples (Fig. 5E) are indicative for shallow water. The top of the section is shows the same lithologies of alternating shale and storm-induced limestone beds as observed in the section DH-1, suggesting a mid to outer shelf setting.

Mineral Mountains. The base of the section (MV, Fig. 6) is dominated by redbeds of terrestrial and probable marginal marine origin (Fig. 7A). The first thick carbonate complex is composed of limestone with brecciated horizons, microbial lamination and birds eye structures (Fig. 7B), which are indicative of a very shallow, restricted marine settings. The top of this complex is consists of a microbe-sponge bioherm complex (see Brayard et al. 2011) that hosts an abundant marine fauna including am-

FIG. 7. Field photographs of the Thaynes Formation of the Minersville locality (section MV). A, Overview photography showing the general succession with transitional continental to marine red beds at the base capped by a peritidal microbial complex which is topped by sponge-microbial bioherms. The largest part of the section is composed of offshore gray marls and limestones. The ridge in the middle part of the picture represents a second level with microbial sponge build-ups developed in outer shelf settings. The far right shows the red beds of the Moenkopi Formation. B, Peritidal limestone with birdseye structures. C, Mass accumulations of Eumorphotis around the Smithian-Spathian transition. D, Ripple-cross bedded sandstones of the Moenkopi Formation intercalated with red siltstones. E, Small sponge-microbial build-ups of the Spathian sponge level. Except A, hammer for scale represents 35 cm.

monoids, thus suggesting a deeper, open marine environment. The overlying interval is characterized by a succession of calcarenitic beds showing bidirectional cross bedding and mud-drapes indicative of a strong tidal influence. The ensuing part of the section records (Fig. 7A) the typical outer shelf facies of the Thaynes Group with intercalated shales and storm-induced limestones. This succession is capped by two occurrences of microbial-sponge bioherms (Fig. 7E). The upper part of the section is composed of siltstones and marls with abundant ripple-cross bedding (Fig. 7D) and small scale hummocky-cross bedding, being suggestive for an upper mid to inner shelf setting. These beds are intercalated with bioclastic grain- and rudstones (Fig. 7C) very similar to the *Eumorphotis*-beds of the Confusion Range. The remainder of the section is represented by marginal marine and continental red beds. The oldest fossiliferous bed which has been included in the analysis is recorded 18 metres below the oldest recorded ammonoid zone of the early Smithian (Figs. 3B and 6). All sampled beds from the upper part of the section (samples MV-4 to MV-12) represent the Smithian-Spathian transition and the lowermost Spathian.

San Rafael Swell. A recent overview on the stratigraphy and sedimentary facies of the Sinbad Formation in the San Rafael Swell (Fig. 8B) is presented in Nützel and Schulbert (2005) and Goodspeed and Lucas (2007). The Sinbad Formation reaches a thickness of about 20 meters in the study area and is mainly composed of some mixed carbonate-siliclastic lithologies of inner shelf settings including carbonate shoals, tidal flats, backshore lagoons and shallow subtidal open marine environments (Goodspeed and Lucas, 2007). Our sampled section was previously studied by Batten and Stokes (1986), Nützel and Schulbert (2005) and Goodspeed and Lucas (2007). The sedimentary facies inferred in these studies is largely supported by our observations (Fig. 9A–D). All samples were derived from beds indicating high energy, shallow marine deposition. However, the sampled horizons adequately represent the palaeocommunities because of a good state of preservation, articulation of bivalves, and wide spectrum of clast sizes arguing against size-sorting (Nützel and Schulbert 2005; Hautmann and Nützel, 2005). Preliminary lithostratigraphical correlation and sparse ammonoid data suggest that this section likely begins in the late middle Smithian (top of *Owenites* beds), and that the uppermost beds represent the late Smithian *Anisibirites* zone and the earliest Spathian (Fig. 3B).

Torrey area. In the area south of Torrey, the Sinbad Formation attains a thickness of about 30 meters. Due to the inaccessibility of the lower part of the Formation, we focussed only on

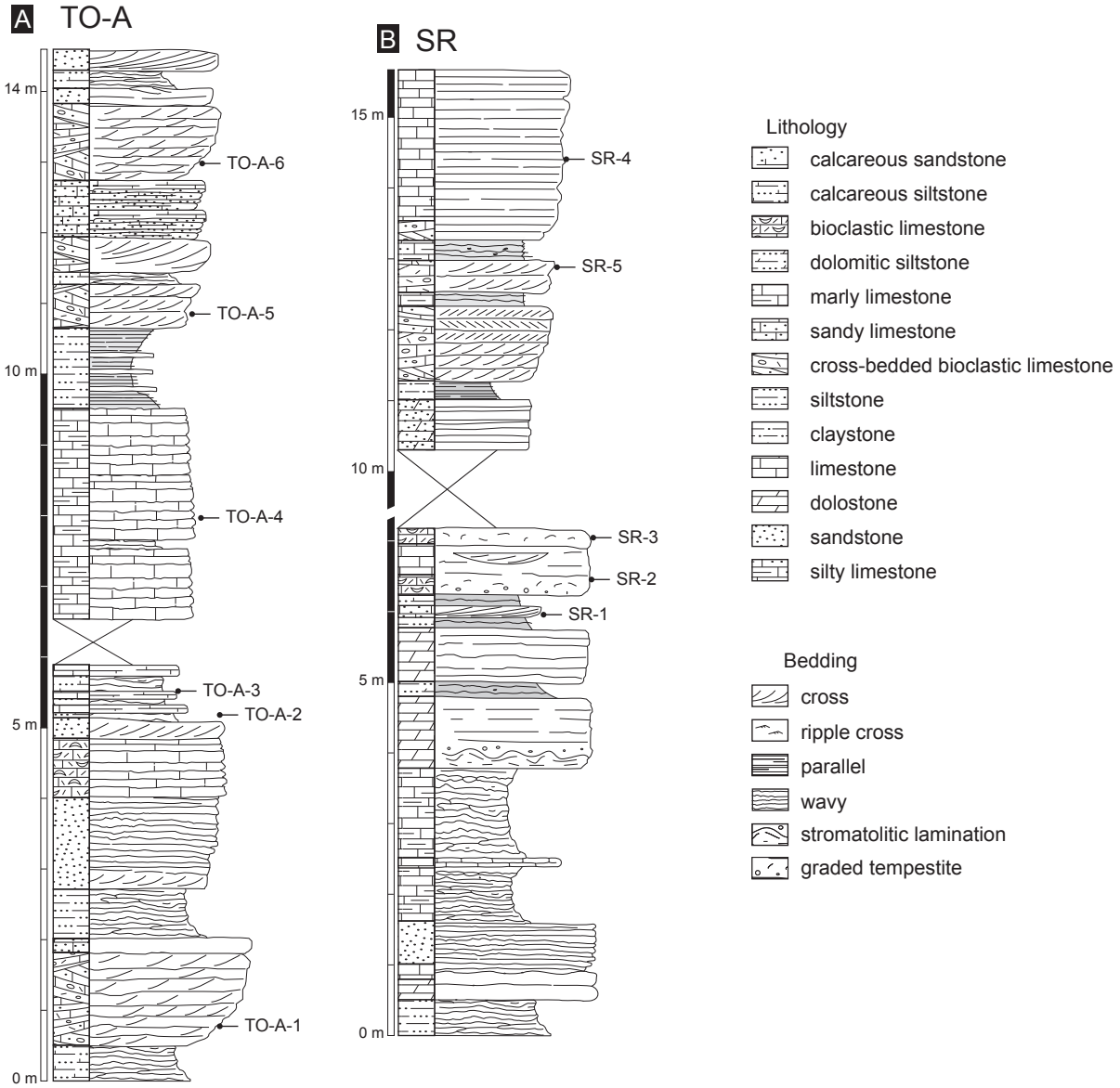

FIG. 8. Sections of the Sinbad Formation. A, Torrey. B, San Rafael Swell.

FIG. 9. Field photographs of the Sinbad Formation (San Rafael Swell, section SR: A–C, Torrey, section TO: D). Hammer for scale represents 35 cm. A, Medium-bedded bioclastic grainstone of the inner shelf environment. B, Medium to thick-bedded grainstones intercalated with fine-grained intervals indicative of the outer and mid- shelf environment. C, Cross-bedded limestones of the inner shelf environment. D, Indistinct trough cross-bedded sandy limestone at the base of the section TO.

the upper 15 meters (Fig. 8A), which correspond to the middle Smithian *Owenites* beds and the upper Smithian *Anasibirites* beds (Fig. 3B). These mixed carbonate-siliciclastic deposits are characterized by cross bedding and tempestitic layers and are thus suggestive of inner and mid shelf environments. Most samples were derived from intercalated, more fine-grained beds that were deposited between fair weather wave base and storm wave base.

SYSTEMATIC PALAEONTOLOGY

Benthic fossils from Lower Triassic rocks are notorious for their poor preservation (Schubert and Bottjer 1995; Hautmann and Nützel 2005). This also applies to much of the material described in this study, which is mainly preserved as internal and external moulds. An in-depth review of the systematic relationship is, thus, hardly possible with the material at hand, but we aimed for species level identification whenever possible. Recent systematic studies of Early Triassic bivalves (e.g. Newell and Boyd 1995; Kumagae and Nakazawa 2009; Hautmann et al. 2011, 2013; Wasmer et al. 2012) were used as a taxonomic framework for the palaeoecological analysis.

Gastropod identification is essentially based on the study of Batten and Stokes (1986), which is the only monographic synopsis of the Sinbad Gastropod fauna and it covers all gastropod species recognized herein. However, supraspecific assignation of many Early Triassic gastropods remains problematic. A revision of taxa described from the Sinbad Formation is currently being carried out by AN.

All specimens are housed in collection of Palaeontological Insitute and Museum at the University of Zürich (PIMUZ).

Bivalves

by Richard Hofmann *and* Michael Hautmann

Class BIVALVIA Linnaeus, 1758
Subclass AUTOLAMELLIBRANCHIATA Grobben, 1894
Superorder PTERIOMORPHIA Beurlen, 1944
Order MYTILOIDA de Férrusac, 1822
Superfamily MYTILOIDEA Rafinesque, 1815
Family MYSIDIELLIDA Cox, 1964

Genus PROMYSIDIEALLA Waller, 2005

Promysidiella sp A.
Figure 10A–D

Material. This species is extraordinarily abundant in all samples from the SR section samples TO-A-1 and TO-A-6. It is furthermore recorded in samples DH-1-9, MV-7, CP-101, and TO-A-2. The description is based on numerous specimens from sample SR-4.

Description. Shell equivalved or slightly inequivalved in cases with right valve being less well inflated. Retrocrescent, notably higher than long, well inflated and variable in form ranging

from slender mytiliform to broader isognomoniform shapes. Anterior margin straight or slightly concave. Posteriordorsal margin rounded. Beak narrow and terminal to slightly projecting. Surface smooth except for irregular growth lines. Internal features not observed.

Discussion. Given the high morphologic variability, we evaluated the possibility that our material represents two distinct species. However, our survey of 30 left and 31 right valves with regard to equivalved/inequivalved condition, shape of the anterior margin, inclination and shape of the posterior auricle, and inflation did not allow distinguishing morphologically separate populations. All observable morphological characters correspond with the diagnosis of *Promysidiella* Waller, 2005 (in Waller and Stanley 2005). Another probably related species could be *Myalinella postcarbonica*, which is described from the Griesbachian–Dienerian Dinwoody Formation (Girty, 1927; see also Hautmann et al. 2011; Hofmann et al. 2013a). Some specimens (e.g. Fig. 10C) of our new collection show close affinities to the material of Girty (1927). However, all specimens observed in the Dinwoody Formation (Hofmann et al. 2013a) have a straight or convex anterior margin. Respective specimens of the Thaynes Group and the Sinbad Formation have a slightly concave anterior margin. Another possible character that is unique to *Promysidiella* is its clearly projecting beak.

Ecology. The equivalved or near-equivalved condition in combination with a straight anterior margin suggests that this species rested byssally attached with its anterior margin on the substrate. Specimens with a somewhat flattened right valve might have lived in a pleurothethtic resting position (Stanley 1972). Regardless of its life position, this species was an epifaunal suspension feeder

Order PTERIOIDA Newell, 1965
Suborder PTERIINA Newell, 1965
Superfamily PTERIOIDEA Gray, 1847
Family BAKEVELLIIDAE King, 1850

Genus BAKEVELLIA King, 1848

Bakevellia cf. *exporrecta* (Lepsius, 1878)
Figure 10E–F

cf. 1878 *Gervillia exporrecta* Lepsius; p. 352, pl. 1, fig. 6a–c.
1908 *Gervillia exporrecta* Lepsius; von Wittenburg, p. 279, pl. 4, fig. 10.
1985 *Bakevellia exporrecta* (Lepsius), Neri and Posenato, p. 92, pl. 1, figs. 6, 7.
2013 *Bakevellia* cf. *exporrecta* (Lepsius); Hautmann et al., p. 270, figs. 5I–Q.

Material. This species rarely occurs in the SR, TO and MV sections. It is however abundant in sections DH-3 and CP. The description is based on numerous well and completely preserved specimens from bed DH-3-2.

Description. Shell slightly twisted, inequivalve, with left valve being more convex than right valve. Outline of valves trapeziform. Byssal gape not observed. Umbo prosogyrate and located on anterior 30 % of the dorsal margin. Beak of left valve slightly projecting above straight hinge line. Shell of both valves covered with fine commarginal growth lines. Internal features not observed.

Discussion. The material described by Hautmann et al. (2013) is conspecific with the material considered in this study. As pointed out in Hautmann et al. (2013), general features agree well with the material figured by Lepsius (1878), but the presence of commissure twisting, which may be relevant in diagnosing species of *Bakevellia*, cannot be inferred from the figured type material. Accordingly, definite species identification is avoided herein as long as the type material has not been critically examined.

Ecology. This species was a filter feeder that pleurothetically rested on the left valve sunken in the substrate (Hautmann et al. 2013).

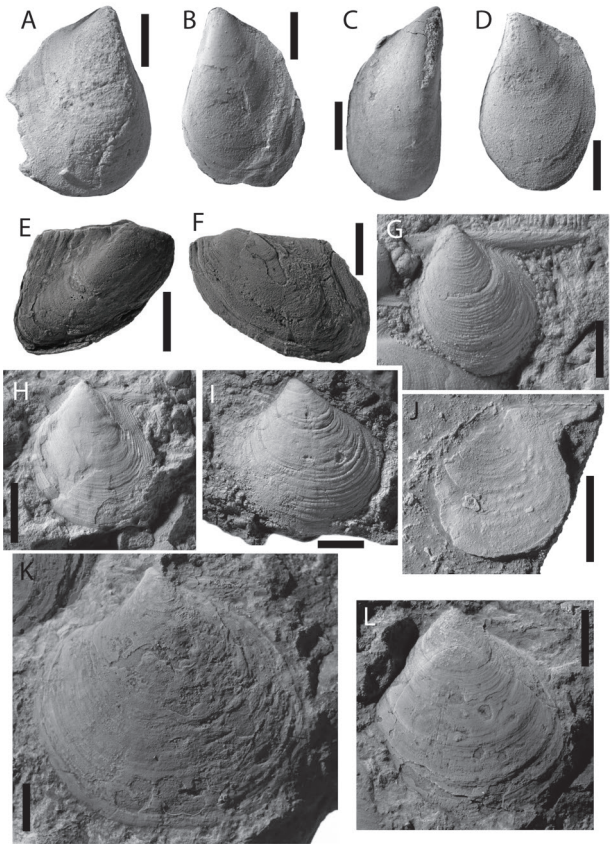

FIG. 10. A–D, *Promysidiella* sp. A from sample SR-4 ,scale bars represent 3 mm if not otherwise indicated A, right valve, PIMUZ 30689. B, left valve, PIMUZ 30687. C, right valve, sample SR-2, scale bat represents 5 mm, PIMUZ 30688. D, left valve, PIMUZ 30690. E–F, *Bakevellia* cf. *exporrecta*, sample DH-3-2, all scale bars represent 5 mm. E, right valve, PIMUZ 30692. F, left valve, PIMUZ 30691. G–L, *Confusionella loczyi*, all scale bars represent 5 mm if not otherwise indicated. G, left valve, sample DH-1-0, PIMUZ 30686, scale bar represents 3 mm. H, left valve, sample DH-1-5, PIMUZ 30685. I, left valve, sample DH-1-5, PIMUZ 30682. J, right valve, sample DH-1-gs1, PIMUZ 30681. K, left valve, sample DH-2-B, PIMUZ 30683. L, left valve, sample DH-2-B, PIMUZ 30684.

Superfamily PTERIACEA Gray, 1847
Family PTERIIDAE Gray, 1847
Genus CONFUSIONELLA gen. nov.

Type species. Pecten loczyi Bittner, 1901b.

Other species. Pseudomonotis laczkoi Bittner, 1901b.

Derivation of name. Referring to the occurrence in the Confusion Range and the fact that it has been presumably confused with other genera (see discussion).

Diagnosis. Pteriid with suborbicular disc and variable obliquity ranging from infracrescent to retrocrescent. Anterior auricle small, triangular, differentiated from disc by auricular sinus; posterior wing well developed, narrow, distally extending far beyond posterior end of disc.
Remarks. The external shell features and the morphology of anterior auricle and posterior wing in particular are highly suggestive for Pteriidae (see diagnosis in Cox et al. 1969). However, because the ligament system is unknown, there remains the remote possibility that the new taxon may alternatively belong to Pterineidae. However, this family is chiefly Palaeozoic and no Early Triassic representatives are known. Although several older works figured material that clearly shows the generic characters described above (see synonymy below), the taxonomic affinity of these specimens has not been correctly recognized. They were commonly assigned to *Pecten, Pseudomonotis,* or *Aviculopecten*, which by that time were understood in a much broader sense than today. With the possible exception of Kumagae and Nakazawa (2009), similar forms have not been reported in more recent studies on Early Triassic bivalves. The excellently preserved material of the Confusion Range gives a hint on the possible cause; the long posterior wing-like projection, which is suggestive of Pteriidae, is prone to mechanical destruction even during short transportation or moderate wave action. If this feature is absent, which is the case in many specimens observed herein (e.g. Fig. 10H–I), the almost equilateral disc resembles entoliids, which are quite abundant in Lower Triassic rocks (see synonymy for examples of possible misidentifications as *Scythentolium* or *Entolioides*).

Confusionella loczyi (Bittner, 1901b)
Figure 10G–L

*1901 *Pecten lóczyi*, Bittner, p. 89, pl. 9, figs. 28–32 (non fig. 30).
1907 *Pseudomonotis Lóczyi* (Bittner); Frech, p. 22, pl. 6, fig. 6.
1908 *Pecten sojalis* n. sp., von Wittenburg, p. 21, pl. 1, fig. 6 non 9.
? 1927 *Aviculipecten disjunctus* n. sp., Girty, p. 437, pl. 30, figs. 22–24.
? 1938 *Pecten* (*Chlamys*) *kryshtofowichi* n. sp., Kiparisova, p. 291, pl. 5. figs. 7–10.
1972 *Scythentolium sojale* Wittenburg, Allasinaz, p. 311, pl. 41, fig.8.
? 2004 *Entolium ussuricus* Bittner, Kashiyama and Oji, p. 213, fig. 8d,e
2009 *Entolium* sp. indet., Kumagae and Nakazawa, p. 165, fig. 144.14.

Revised diagnosis. Confusionella with very regular, fine but distinct commarginal ribs. Radial ornament absent.

Material. Frequently recorded in all samples DH-1-0 to DH-1-9. The description is based on well preserved specimens (PIMUZ 30686, 30685, 30682, 30681, 30683, 30684).

Description. Shell slightly inequivalve, with left valve being more convex than right valve. Disc suborbicular to ovate with apical angle of ca. 85°. Shell infracrescent to retrocrescent. Hinge margin straight, with orthogyrous to prosogyrous umbo projecting above hinge line. Umbo located on anterior 30 % of dorsal margin. Anterior auricle triangular, with well developed auricular sinus. Posterior wing narrow and strongly elongated. Disc and auricles covered with regular, closely spaced, very fine but disctinct commarginal ribs.

Discussion. A probably closely related species is what Bittner introduced as *Pseudomonitis laczkoi*, which is very similar with respect to the general shape and configuration of the auricles. It differs from *C. loczyi* in showing a distinct radial ornament (see also Frech 1907). It is very likely that *Pseudomonitis laczkoi* pertains to the genus *Confusionella* as well.

The very conspicuous regular commarginal sculpture and the discoid shape can easily be recognized in hitherto described material from the western US (Girty 1927), and Ussuri Bay (Kiparisova 1938; Kumagae and Nakazawa 2009). Having studied the material from the Confusion Range, some 'entoliid' bivalves (e.g. Alassinaz 1972; Kashiyama and Oji 2004; Kumagae and Nakazawa 2009) described in the literature may also belong to *Confusionella*. If our assignation is correct, this genus would be very common in Smithian strata such as the Hidegkut Sandstone of the Balaton Region (Bittner 1901b), the Campil Member of the Dolomites (Wittenburg 1908; Alassinaz 1972), and the Thaynes Group (Girty 1927; this paper).

Ecology. The flat right valve and shallow byssal sinus suggest that *Confusionella* was a bysally attached epifaunal suspension feeder.

Order PECTINOIDA Gray, 1854
Suborder PECTININA Waller, 1978
Superfamily AVICULOPECTINOIDEA Meek and Hayden, 1864
Family ASOELLIDAE Begg and Campbell, 1985

Genus LEPTOCHONDRIA. Bittner, 1891

Leptochondria occidanea (Meek, 1877)
Figure 11A–C

*1877 *Aviculopecten occidaneus* Meek, p. 96, pl. 12, figs. 13–13b.
1909 *Pecten viezzensis*, Wilckens, p. 147, pl. 5, fig. 25.
1927 *Monotis superstricta* var. *parksi*, Girty, 1927, p. 441, pl. 30, figs. 20, 21.
1972 *Leptochondria viezzensis* (Wilckens), Allasinaz, p. 259, pl. 31, figs. 5–9.
1995 *Leptochondria occidaneus* (Meek), Newell and Boyd, p. 70, figs. 51.3–519.
2012 *Leptochondria viezzensis* (Wilckens), Wasmer and Hautmann, p. 1058, figs 7K–R.

Material. Present in all samples of the Disappointment Hills sections except DH-1-gs2, DH-1-5 and DH-1-5. Particularly abundant in sample DH-1-3. Present in DV-5 of the Dog Valley section. The description is based on abundant well preserved specimens from section DH-1 and sample CP-8.

Description. Disc almost equilateral, orbicular, slightly higher than long. Left valve feebly convex with orthogyrate umbo slightly projecting above straight dorsal margin. Umbo located at anterior 40 % of hinge line. Anterior auricle well demarcated from disc, with shallow auricular sinus. Posterior auricle not preserved. Valves covered with up to 45 simple radial ribs, rounded in shape. Few second order ribs distally inserted by intercalation. Radial ornamentation fading out towards anterior and posterior margin including both auricles. Very weak and dense commarginal riblets present on the entire valve. Internal features unknown. Right valve not observed.

Discussion. The specimens from the Thaynes Group and Sin-

bad Formation agree well with *L. occidanea* figured in Newell and Boyd (1995) including a relatively pronounced anterior auricular sinus, a large posterior auricle, and second order ribs inserted by intercalation. In terms of ornamentation, *L. viezzenensis* is virtually indistinguishable from *L. occidanea* but it has been suggested (Wasmer et al. 2012) that the sinuate posterior left auricle is a diagnostic feature of *L. viezzenensis*. However, published material which has subsequently been assigned to *L. occidanea* (e.g. *Monotis superstricta* var. *parksi* Girty 1927) shows the same morphology, which is also the case for material described herein (Fig. 11C). Accordingly we suggest *L. viezzennsis* is a junior synonym of *L. occidanea.* As pointed out by Wasmer et al. (2012), *Leptochondria bittneri* (Kiparisova 1938) lacks a sinuate posterior auricle, but is otherwise very similar to *L. occidanea. L. occidanea* is very common in the Early Triassic of the western US, especially throughout the Smithian and Spathian time interval (Newell and Boyd 1995).

Ecology. The genus has a flat right valve with byssal notch (not observed in the present material), which suggest that *Leptochondria* was a byssaly attached epifaunal filter feeder resting pleurothetically on the right valve.

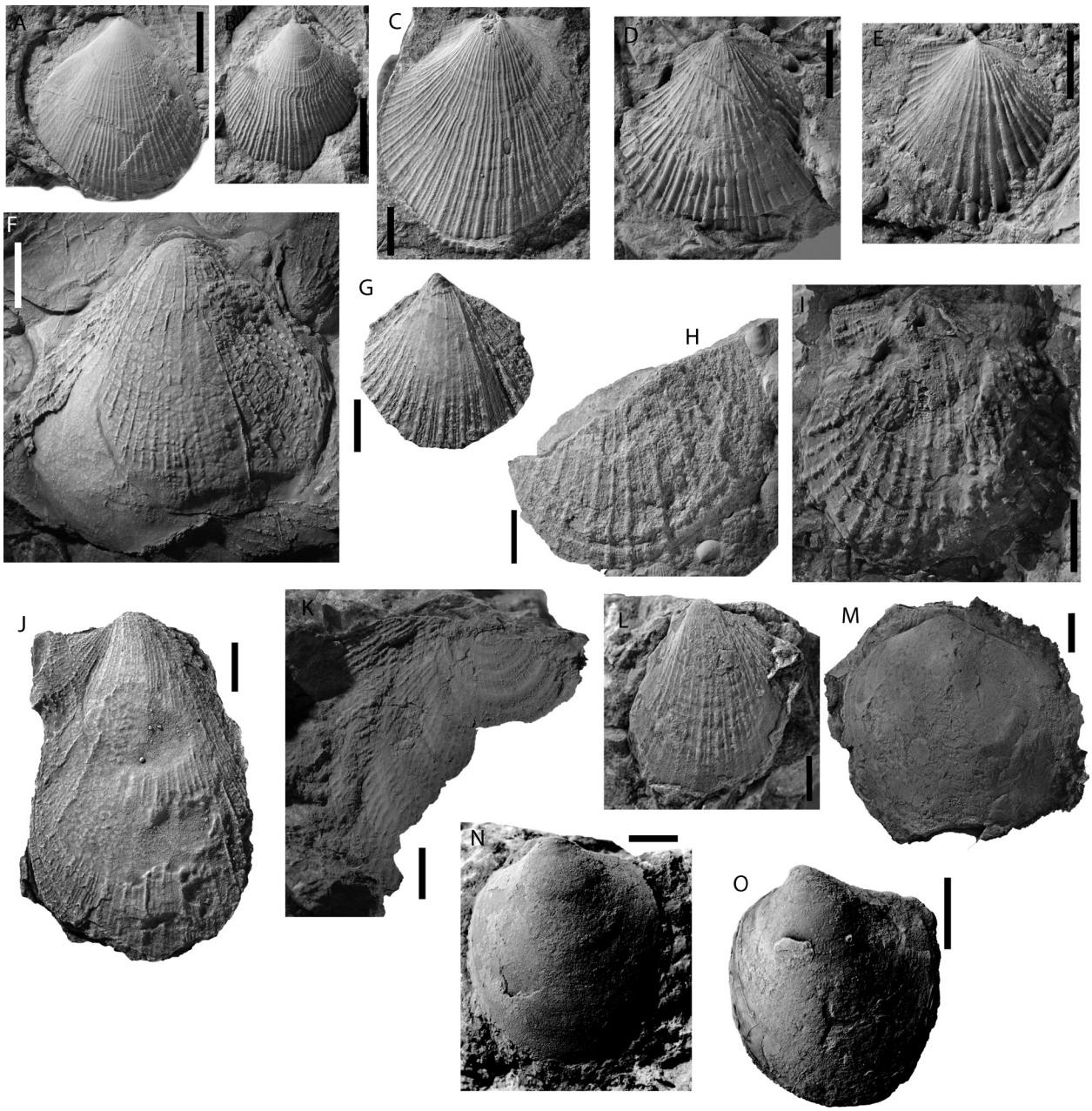

FIG. 11. A–C, Leptochondria occidanea, all scale bars represent 5 mm. A, left valve, sample DH-1-4, PIMUZ 30677. B, left valve, sample DH-1-4, PIMUZ 30678. C, left valve, sample CP-8, PIMUZ 30679. D–E, Leptochondria xijinwulanensis, D, left valve, sample DH-1-5, PIMUZ 30676, scale bar represents 5 mm. E, left valve, sample DH-1-9, PIMUZ 30680, scale bar represents 3 mm. F, Eumorphotis ericius, left valve, float at the top of section DH-3, PIMUZ 30667, scale bar represents 10 mm, G–H, Eumorphotis beneckei. G, left valve, sample DH-2-B, PIMUZ 30668, scale bar represents 5 mm. H, fragment of a left valve, sample DH-1-2, PIMUZ 30669, scale bar represents 10 mm. I, Eumorphotis hinnitidea, left valve, sample CP4, PIMUZ 30666, scale bar represents 10 mm. J–L, Eumorphotis multiformis, all scale bars represent 5 mm. J, left valve, sample DV-2, PIMUZ 30671. K, right valve, sample DH-3-1, PIMUZ 30670. L, left valve, sample MV-10, PIMUZ 30672. M, Pernopecten? sp. A, right valve, sample TO-A-5, PIMUZ 30673, scale bar represents 10 mm. N–O, Crittendenia? sp. A, all scale bars represent 5 mm. N, left valve, sample SR-3, PIMUZ 30674. O, left valve, DH-2 B, PIMUZ 30675.

Leptochondria xijinwulanensis Sha 1995
Figure 11D–E

*1995 ?*Leptochondria xijinwulanensis* sp. Sha, p. 94, pl. 26, figs 1–6.
1995 *Leptochondria* cf. *albertii* (Goldfuss); Sha, p. 92, pl. 26, fig. 7.
1995 *Leptochondria albertii* (Goldfuss); Sha, p. 92, pl. 26, fig. 9.
1995 *Leptochondria* sp., Sha, 94, pl. 26, fig. 24.
1996 ?*Leptochondria xijinwulanensis* (Sha, 1995); Sha and Grant-Mackie, pl. 3, fig. j.
2012 *Leptochondria xijinwulanensis* (Sha, 1995); Wasmer and Hautmann, p. 1058, figs 7D–J.

Material. Two left valves DH-1-5 and one left valve in DH-1-9. The description is based on the figured specimens PIMUZ 30676 and PIMUZ 30680).

Description. Left valve subcircular, convex, nearly equilateral and slightly higher than long. Auricles subequal in size, obtuse and well demarcated from the disc. Anterior auricle subtriangular. Posterior auricle with shallow sinus. Beak not projecting above straight dorsal margin. Umbo orthogyrate to slightly prosogyrate, located near the mid of dorsal margin. Internal features unknown. Left valve covered with up to 30 simple, relatively widely spaced sharp radial ribs. Second order ribs are distally inserted by intercalation. Very weak, commarginal riblets present, most notably developed on posterior and anterior side of disc. Right valve and shell interior not observed.

Discussion. The specimens from the Confusion Range agree very well with features of *Leptochondria xijinwulanensis* Sha, 1995 from the Early Triassic of western China. Most notably, the characteristic ornamentation with comparably few, widely spaced and pronounced radial ribs is virtually indistinguishable from the material figured by Sha (1995) and Sha and Grant-Mackie (1996). Wasmer et al. (2012) reported the same species from the Spathian of Pakistan and noted a variety of morphological features, which further lends support to the species identification of the material presented herein. Sha (1995) figured some specimens of *Leptochondria*, which he assigned to *L*. cf. *albertii* (pl. 26, fig. 7), *L. albertii* (pl. 26, fig. 9), and *L.* sp. (pl. 26, fig. 24). We note that all of these specimens closely resemble the type material of *L. xijinwulanensis* in having widely spaced and sharp radial ribs on the shell exterior, which is not found in any other species of *Leptochondria* (Wasmer et al. 2012). A possible criterion for separating these forms on the species level could be the presence of commarginal riblets in '*L. albertii*" and '*L.* sp" in Sha (1995). However, our material and that described by Wasmer et al. (2012) suggests that this feature is very variable among specimens that are otherwise indistinguishable. This indicates that the development of commarginal ribs or riblets may rather reflect taphonomic and diagnetic effects as well as potential intraspecific variation and, thus, could not be considered as diagnostic criterion for species differentiation. We follow Wasmer et al. (2012) and unite all *Leptochondria* with this type of ornamentation under *L. xijinwulanensis.*

Ecology. As for *L. occidanea*

Family HETEROPECTINIDAE Beurlen, 1954

Genus EUMORPHOTIS Bittner, 1901a
*1901 *Eumorphotis*, Bittner, p. 56.
1983 *Neomorphotis*, Yin and Yin [in Chinese]
2009 *Neomorphotis* Fang et al., p. 34. [English translation of original diagnosis]

Discussion. Eumorphotis was erected by Bittner (1901a) to accommodate species of aviculopectinids with well-developed auricles and a flat right valve that were previously placed in *Pecten* or *Pseudomonotis*. *Neomorphotis* Yin and Yin, 1983 agrees well with all typical features of *Eumorphotis* except for its notably large size and Spondylus-like ornamentation (Fang et al. 2009). However, size is generally a poor criterion for distinguishing between taxa. Furthermore, Bittner (1901a) already pointed out that *Eumorphotis* shows a great variability and intergradational stages regarding its ornamentation, including what has been suggested as diagnostic for *Neomorphotis*. Accordingly, we consider *Neomorphotis* a junior synonym of *Eumorphotis*.

Eumorphotis beneckei (Bittner, 1901a)
Figure 11G–H

*1901 Pseudomonotis beneckei, Bittner, p. 574, pl. 23, fig. 5.
1986 *Eumorphotis beneckei* (Bitter, 1901) Broglio Loriga and Mirabella, p. 271, pl. 3, figs. 3–6.
2008 *Neomorphotis compta* (Goldfuss, 1838) Posenato, p. 101, figs. 4A–G.

Material. Two left valves in sample DH-2-B and one left valve in sample DH-1-5. The description is based on two specimens (PIMUZ 30668, 30669).

Description. Left valve moderately inflated, presumably retrocrescent. Umbo orthogyrate and projecting above hingeline. Auricles not preserved. Radial ornamentation with about 15 strong nodular first order ribs. A set of numerous (up to seven) fine second order ribs between each two first order ribs. Right valve and internal features not observed.

Discussion. E. beneckei is distinguished from all other described species of *Eumorphotis* with strong squamose radial ribs (see discussion to *E. ericius* and *E. hinnitidea*) by numerous delicate second order ribs. The type specimen has been described from the Anisian of the Dolomites (Bittner 1901a). Posenato (2008) placed *E. beneckei* in synonymy of *Ostrea compta* Goldfuss 1838, based on the striking similarity in ornamentation. However, the original specimen figured by Goldfuss (1838) shows little diagnostic characters in addition to ornamentation, which gave rise to much confusion about the proper definition of this species, summarized in Posenato (2008) and Hautmann and Hagdorn (2013). We therefore prefer regarding *Ostrea compta* as a nomen dubium and including our material in the well-defined *E. beneckei.*

Ecology. The flat right valve and the byssal sinus in the left anterior auricle suggest that *E. beneckei* was epibyssaly attached resting on its flat right valve.

Eumorphotis ericius Hautmann et al., 2013
Figure 11F

?1908 *Pseudomonotis beneckei* Bittner, von Wittenburg, p. 29, pl. 4, fig. 1.
?1908 *Pseudomonotis reticulatus* Richthofen; von Wittenburg, p. 30, pl. 2, figs. 8, 9.
*2013 *Eumorphotis ericius* n. sp. Hautmann et al., p. 275, figs. 6H–L.

Material. Frequently observed in beds around Smithian–Spathian boundary interval. The description is based on several well preserved specimens from sample CP-3 and CP-5.

Description. Large, well inflated left valve, higher than long, usually infracrescent, slightly retrocrescent in early growth stages. Umbo slightly prosogyrate, near midpoint of straight dorsal margin. Anterior auricles with shallow auricular sinus, posterior auricles wide. Radial sculpture well developed, with numerous (up to 70) squamose first order ribs and weeker second order ribs inserted by intercalation. Ribs of third order rarely observed. Internal features and right valves not observed.

Discussion. This species is easily recognized by its numerous squamose ribs. It has been described from the lower Spathian Virgin Formation of the western US (Hautmann et al. 2013) and is abundant in coeval rocks of the Thaynes Group of the investigated area. It occurs in high abundances in the Confusion Range and at the Mineral Mountains section and forms paucispecific bedding plane assemblages within the basalmost Spathian. This species is also a typical constituent of diverse benthic inner shelf assemblages of the Virgin Formation (Hofmann et al. 2013b). It has also been tentatively described from the Griesbachian to Dienerian Dinwoody Formation of Montana (Hofmann et al. 2013a). In the Werfen Formation of the Dolomites, it may be represented by '*Pseudomonotis beneckei*" of Wittenburg (1908, pl. 4, fig. 1) that closely resembles the type material from the Virgin Formation (Hautmann et al. 2013) in general shape and the characteristic sculpture. Another specimen described as *Pseudomonotis reticulatus* by Wittenburg (1908, pl. 2, figs. 8, 9) is also very similar to *E. ericius*. However, the type specimen of *Eumorphotis reticulata* (=*Spondylus reticulatus* in Richthofen, 1860) has never been figured. The description by Richthofen (1860) that has been cited by Wittenburg (1908) does not match completely the Wittenburg material. For instance, the figured specimen of *Pseudomonotis reticulatus* is neither obliquely-oval nor does it possess three to four secondary ribs between the primary ribs towards the margin (Richthofen1860). Accordingly, the affinity of Wittenburg's *Pseudomonotis reticulatus* and, hence, the relationship of *E. ericius* to *E. reticulatus* (Richthofen 1860) remains unclear without an examination of the type material of the Richthofen (1860) material.

Ecology. As for *E. beneckei.*

Eumorphotis hinnitidea (Bittner, 1898)
Figure 11I

*1898 *Pseudomonotis hinnitidea* Bittner, p. 716, pl. 15 , figs. 8–10.
1908 *Pseudomonotis spinicosta* von Wittenburg, p. 76, figs. 6, 7.
1986 *Eumorphotis hinnitidea* (Bittner), Broglio Loriga and Mirabella, p. 266, pl. 4, figs. 1–3.

Material. One left valve from sample CP-4

Description. Relatively large, feebly inflated left valve, subcircular in outline and slightly procrescent. Umbo orthogyrate, located in the midst of straight dorsal margin. Anterior auricle with shallow sinus. Posterior auricle obtuse. One order of about 25 strong spinose radial ribs. Faint commarginal riblets forming a reticulate pattern by intersection with the radial ribs.

Discussion. This species is characterized by its circular outline and comparably few, robust, squamose radial ribs. We follow the revision of Broglio Loriga and Mirabella (1986) who suggested that *E. spinicosta* is a junior synonym of *E. hinnitidea*. The similar species *E. ericius* is notably higher than long and has more ribs intercalated in two ranks. This is the first report of *E. hinnitidea* from Panthalassa, where it is confined to the lowermost Spathian. In the Tethys, this species has been observed in Smithian and Spathian strata Broglio Loriga and Mirabella, 1986)

Ecology. As for *E. beneckei.*

Eumorphotis multiformis (Bittner, 1899)
Figures 11J–L

*1899 *Pseudomonotis multiformis*; Bittner, p. 10, p1. 2, figs. 15–22.
1942 *Eumorphotis multiformis* (Bittner, 1899); Newell and Kummel, p. 957, p1. 2, figs. 10, 11.
1963 *Eumorphotis multiformis* (Bittner, 1899); Ciriacks, p. 77, pl. 15, figs. 13, 15.
1963 *Eumorphotis multiformis regularaecosta* Kiparisova; Ciriacks, 1963, p. 77, pl. 15, fig. 14.
2009 *Eumorphotis multiformis* (Bittner, 1899); Kumagae and Nakazawa, p. 162, fig. 144.17, (cum synonymis).

Material. Rather rare in samples DV-2, DH-3-1, DH-3-3, SR-1, MV-3, MV-5, MV-6 and MV-10. The description is based on several well preserved specimens from DV-2, DH-3-1.

Description. Left valve weakly to moderately inflated, almost equilateral, infracrescent. Umbo orthogyrate to slightly prosogyrate, slightly projecting above straight hinge line and placed centrally. Anterior auricle well demarcated from disc, with shallow auricular sinus. Posterior auricle not observed. Left valve covered with three orders of radial ribs being irregularly intercalated.

Discussion. E. multiformis is characterized by multiple orders of intercalated, mostly smooth radial ribs in variable configurations. However, no clear distinction of discrete morphotypes has been established so far. Earlier workers introduced a number of varieties or subspecies of *E. multiformis* (see Broglio Loriga and Mirabella 1986 for overview), but more recent taxonomic practice (see Kumagae and Nakazawa 2009) considers the various subspecies of *E. multiformis* as synonyms of a highly variable species. *E. multiformis* has a cosmopolitan distribution and is reported from the Griesbachian (Ciriacks 1963), Dienerian (Broglio Loriga and Mirabella 1986) and the Spathian (Hautmann et al. 2013).

Ecology. As for *E. beneckei.*

Family DELTOPECTINIDAE Dickins, 1957

Genus CRITTENDENIA Newell and Boyd, 1995

Crittendenia? sp.
Figure 11N–O

Material. Rarely recorded in samples DH-2B, DV-3, SR-1, SR-2, SR-3. The description is chiefly based on some well preserved left valves from sample SR-3.

Description. Left valve suborbicular to slightly retrocrescent, slightly higher than long and distinctly inflated. Umbo prominent, prosogyrous, with beak projecting well beyond hinge line.

Posterior auricle poorly differentiated from disc. Valves general smooth except from very faint commarginal growth lines. Right valve not observed.

Discussion. Newell and Boyd (1995) introduced the genus *Crittendenia* to accomodate species of the *Claraia decidens*-group of Ichikawa (1958) which are characterized by a well inflated left valve and absent or very weak ornamentation. *Crittendenia*, as defined by Newell and Boyd (1995), applies to species with an almost flat right valve, as exemplified by the type species *Crittendenia kummeli*. Newell and Boyd also included material from the Salt Range in this species, which however has recently been placed in *Eobuchia punjabensis* (Wasmer et al. 2012). The left valve of *Crittendenia* is virtually indistinguishable from that of *Eobuchia* but its right valve clearly differs in having a strongly prosogyrate umbo and a very wide byssal notch below the anterior auricle (Wasmer et al. 2012). Accordingly, without knowledge on the morphology of the right valve, the material at hand could be assigned to either of both genera. Because *Crittendenia* has previously been reported from the Smithian of the Thaynes Group (Newell and Boyd 1995), we provisionally place our material in this genus.

Ecology. Crittendenia was an epifaunal, byssally attached filter feeder (Wasmer et al. 2012).

Suborder ENTOLIIDINA Hautmann, 2011
Superfamily ENTOLIOIDEA Korobkov, 1960
Family ENTOLIIDAE Korobkov, 1960

Remarks. As noted by Hautmann et al. (2013), splitting the Entoliidae into various families and subfamilies is not justified on the basis of observed morphological differences.

Genus PERNOPECTEN Winchell, 1895

Pernopecten? sp. A
Fig. 11M

Material. Rarely recorded in samples TO-A-4, TO-A-5 and TO-B-5. The description is based on a comparatively well preserved right valve from sample TO-A-5 (PIMUZ 30673) and poorly preserved left? valves from the same sample.

Description. Shell fairly large, subcircular in outline, orthocline, and equilateral. Left valve feebly inflated. Auricles not observed in left valves. Right valve feebly inflated, with small beak not projecting above hinge margin, placed at or near the midst of the straight hinge line. Auricles without scrolls, anterior auricle small, rounded, with very shallow sinus, posterior auricle obtuse and slightly larger than anterior one. Surface of both valves smooth.

Discussion. As noted by Waller (2006), *Pernocpecten* represents the only entoliid genus in which projecting auricles (scrolls in Waller 2006) occur in the left valve and not in the right valve as is the case in all other entoliids that developed this feature. *Entolioides* Allasinaz, 1972 lacks scrolls in both valves, but this genus differs in having a well-developed radial ornamentation. Based on specimens from the Thaynes Group of Nevada, Idaho and Montana, Newell and Boyd (1995) erected *Entolioides utahensis*, in which the right valve is similar to the material presented herein. Left valves of this species should show a distinct radial sculpture – a trait considered as typical for the genus *Entolioides* by Allasinaz (1972) and Newell and Boyd (1995, p. 76). We did not observe radial ornamentation of this kind in our material. Although right/left valve determination is uncertain in most cases, we regard it unlikely that left valves are completely lacking in our samples. We therefore tentatively place our material in *Pernopecten* rather than in Entolioides.

Pernopecten is a chiefly late Palaeozoic genus (Newell 1937), but it also ranges into the Early Triassic (Posenato et al. 2005; Waller 2006; Hautmann et al. 2013). Waller (2006) suggested that *Pernopecten* gave rise to all younger representatives of the Pectinoidea during the Early Triassic, but this hypothesis was rejected by Hautmann (2010) and Carter and Hautmann (2011) who assumed a diphyletic origin of the entolioid and pectinoid clades.

Ecology. Pernopecten was a free lying epifaunal filter feeder probably capable of swimming by rapidly clapping its valves (Stanley 1972; Hautmann 2004).

Subclass HETEROCONCHIA Hertwig, 1895
Superorder PALAEOHETERODONTA Newell, 1965
Order MODIOMORPHOIDA Newell, 1969
Superfamily MODIOMORPHOIDEA Miller, 1877
Family KALENTERIDAE Marwick, 1953

Genus PERMOPHORUS Chavan, 1954

Permophorus cf. *bregeri* (Girty, 1927)
Figures 12A–D

cf. *1927 *Pleurophorus bregeri* n. sp.; GIRTY, p. 445, pl. 30, figs. 40, 41.
cf. 1927 *Pleurophorus similis* n. sp.; GIRTY, p. 446, p1. 30, figs. 38, 39.
cf. 1927 *Pleurophorus rotundus* n. sp.; GIRTY, p. 446, pl. 30, figs. 42, 43.
1963 *Permophorus*? *bregeri* (Girty); CIRIACKS, p. 83, pl 16, figs 8, 9

Material. Recorded in relatively high numbers in sample SR-4. Description is based on all specimens shown in Fig. 12.

Description. Shell equivalve, subrectangular in outline, considerably longer than high. Umbo almost terminal, strongly prosogyrate, with very small beak slightly projecting above dorsal and anterior margin. Dorsal and ventral margin straight and subparallel. Posterior margin rounded. Anterior margin truncated with small lunule. Straight carina running from the umbo towards the posteroventral corner of shell. Faint radial ridge on the posteriordorsal part of the valves.

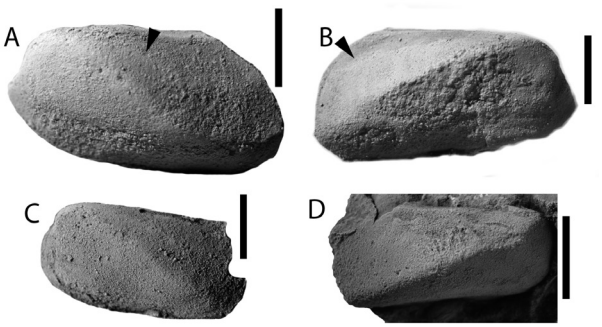

FIG. 12. *Permophorus* cf. *bregeri*, all scale bars represent 3 mm. Black arrows point to the faint second diagonal ridge. A, left valve, sample SR-4, PIMUZ 30712. B, right valve, sample SR-4, PIMUZ 30713. C, left valve, sample SR-4, PIMUZ 30714. D, right valve, sample SR-4, PIMUZ 30715.

Discussion. We follow Ciriacks (1963) who suggested that all three species of '*Pleurophorus*' (*P. similis*, *P. bergeri*, and *P. rotundus*) represent the species of *Permophorus bregeri* (see also Hofmann et al. 2013a, for discussion). Given the considerable variability of *P. bregeri*, the material from the Sinbad Formation is best placed within this species. However, it is noted that the diagnonal ridge in some specimens is slightly S-shaped (Fig. 12C) and that the specimens from the Sinbad Formation are somewhat more elongated.

We note that the external morphology of this species is very similar to Middle Triassic *Protopis* Kittl, 1904, provisionally placed in the modiomorphoid family Healeyidae Hautmann, 2008 by Hautmann (2008). Placement of Protopis in Permophoridae appears a possible alternative, depending on the presence or absence of a comparable hinge dentition, which is currently unknow in *Protopis*.

Ecology. The modioliform shape of *P. bregeri* suggests an endobyssate mode of life (cf. Stanley 1972).

Order UNIONOIDA Stoliczka, 1871
Superfamily ANTHRACOSIOIDEA Amalitsky, 1892
Family ANTHRACOSIIDAE Amalitsky, 1892

Genus UNIONITES Wissmann, 1841 (in Münster)

Remarks. We follow the revision of Geyer et al. (2005) that indicates assignment of *Unionites* to Anthracosiidae Amalitsky, 1892. Most reports of Early Triassic *Unionites* are based on external morphological characters, which are of limited value in terms of genus identification. Our material is no exception in this respect, and thus, generic assignment to *Unionites* represents conventional practice rather than new morphological information.

Unionites cf. *canalensis* (Catullo, 1846)
Figure 13A–B

cf. *1846 *Tellina canalensis*; Catullo, p. 56, pl. 4, fig. 4.
1859 *Tellina* (*Myacites*) *canalensis* Catullo, 1846; Schauroth, p. 327, pl. 2, fig. 17.
1923 *Anodontophora canalensis* (Catullo, 1846); Diener, p. 230 (cum synonymis).
1963 *Unionites canalensis* (Catullo, 1846); Ciriacks, p. 81, pl. 16, figs. 11, 12.
2009 *Unionites canalensis* (Catullo, 1846); Kumagae and Nakazawa, p. 166, figs. 145.1–145.4 (cum synonymis).

Material. Recorded in samples DV-1, DV-2, SR-4 and TO-A-1. Preserved as internal and external moulds. The description is based on relatively well preserved external moulds from SR-4 (PIMUZ 30700, 30969).

Description. Shell equivalved, outline elongate subelliptical. Ventral margin nearly straight. Umbones prosogyrous, with beak projecting above dorsal margin and located approximately in the mid or slightly shifted towards the anterior side of dorsal margin. More or less well developed umbonal ridge. Posterior margin truncated. Anterior margin rounded. Internal features unknown.

Discussion. Unionites canalensis is a widely reported species from Lower Triassic rocks and is distinguished from the similar *U. fassaensis* by its more elongated outline and more pronounced umbonal ridge (Kumagae and Nakazawa 2009). Ciriacks (1963, p. 82) emphasized a medial location of the umbones in his material of *U. canalensis*, but other descriptions report a position of the umbones in the anterior part of the shell (von Schauroth 1859; Hautmann et al. 2013). In the material at hand, the position of the umbones is variable but generally anterior to the center of the dorsal margin (compare Figs. 13 A and B). Given the lack of diagnostic characters in addition to the general shape, however, the taxon remains poorly defined.

Ecology. Unionites canalensis was a shallow infaunal suspension feeder (e.g. Hautmann et al. 2013).

Unionites cf. *fassaensis* (Wissmann [in Münster]), 1841
Figures 13C–D

cf. *1841 *Myacites fassaensis* Wissmann, 1841, p. 9, pl. 16, figs. 2a–c.
1963 *Unionites fassaensis* (Wissmann); Ciriacks, p. 82, pl. 16, fig. 13.
?1963 *Unionites breviformis* (Spath); Ciriacks, p. 81, pl. 16, figs. 14, 15.
2009 *Unionites fassaensis* (Wissmann); Kumagae and Nakazawa, p. 167, figs 144.5–144.9 (cum synonymis).

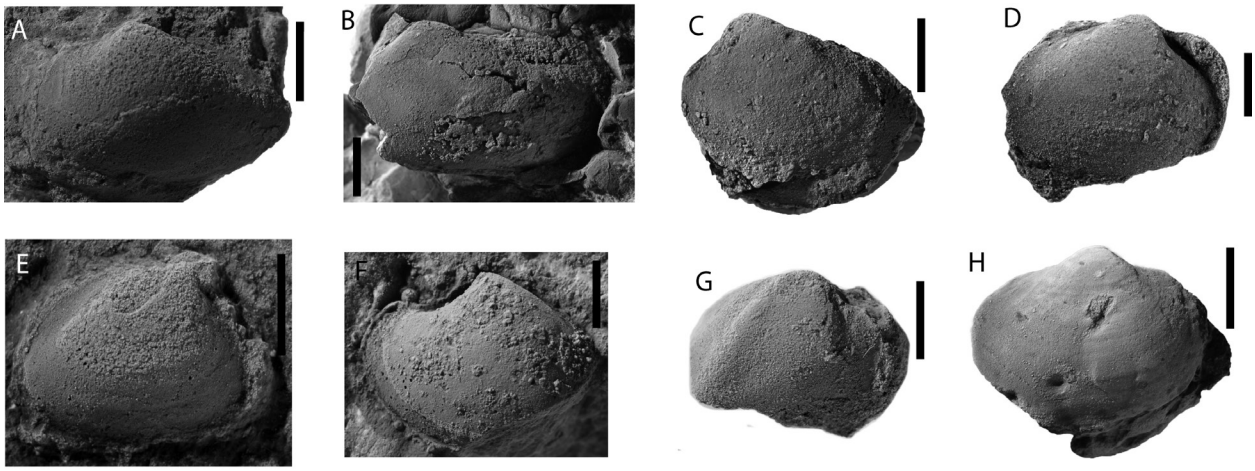

FIG. 13. A–B, *Unionites* cf. *canalensis*, all scale bars represent 5 mm. A, left valve, sample SR-4, PIMUZ 30700. B, left valve, sample SR-4, PIMUZ 30969. C–D, *Unionites* cf. *fassaensis*. C, left valve, sample SR-2, PIMUZ 30699, scale bar represents 5 mm. D, right valve, sample SR-2, PIMUZ 30698, scale bar represents 3 mm. E, *Neoschizodus laevigatus*, right valve, sample SR-4, PIMUZ 30695, scale bar represents 3 mm. F, *Sinbadiella pygmaea*, right valve, TO-A-2, PIMUZ 30693, scale bar represents 3 mm. G, *Sementiconcha recuperator*, right valve, SR-4, PIMUZ 30694. scale bar represents 3 mm. H, *Unicardium* sp. A, left valve, DH-1-gs2, PIMUZ 30697. scale bar represents 5 mm.

Material. Rarely recorded in samples of the TO-A, SR, DV, DH-3, DH-1, and MV sections. The description is based on comparatively well preserved external moulds from sample SR-2 (PIMUZ 30699).

Description. Shell equivalve, subelliptical in outline, with prosogyrous umbones projecting above dorsal margin. Beaks located approximately on anterior 40% or less of dorsal margin. Posteriordorsal margin almost straight, anterior margin rounded. Internal features and sculpture not observed.

Discussion. Unionites fassaensis is among the most widely reported bivalve species of the Early Triassic. The wide geographic range and the dominance of this species may partly result from its poor taxonomic definition. However, in contrast to strata of the immediate post extinction interval (i.e. the Griesbachian), where it occurs in tremendous numbers (Schubert and Bottjer 1995; Hofmann et al. 2013a), it appears to recede in later time intervals. At least in the western US, this species is considerably rare in the Smithian (this study) and the Spathian (Hofmann et al. 2013b).

Ecology. As for *Unionites canalensis.*

Order TRIGONIOIDA Dall, 1899
Superfamily MYOPHORIOIDEA Bronn, 1849
Family MYOPHORIIDAE Bronn, 1849

Genus NEOSCHIZODUS Giebel, 1855

Neoschizodus laevigatus (Ziethen, 1830)
Figure 13E

*1830 *Trigonia laevigata*; Ziethen, p. 94, pl. 71, figs 2, 6.
1923 *Myophoria laevigata* (Ziethen); Diener, p. 174, (cum synonymis)
1963 *Myophoria laevigata* (Ziethen, 1830); Ciriacks, p. 82, pl. 18, figs. 18, 19.
2009 *Neoschizodus* cf. *laevigatus* (Ziethen); Kumagae and Nakazawa, p. 170, figs. 145.10–145.15

Material. Rarely recorded in samples SR-4, MV-12, and TO-A-6. The description is based on a right valves preserved as mould from sample SR-4 (PIMUZ 30695).

Description. Shell equivalved, moderately inflated, subtrigonal, slightly longer than high and inequilateral. Umbo slightly prosogyrate. Anterior and posterior margin truncated. Shell with sharp umbonal ridge. Surface smooth.

Discussion. The material at hand agrees well in all external morphological features of Neoschizodus laevigatus, which is a widely reported species in Lower and Middle Triassic rocks. *N. laevigatus* shows a high variability in its morphological characters. Accordingly, it is unclear whether the wide geographic and stratigraphic range of this species is a real phenomenon or rather an effect of its morphological indistinctness.

Ecology. N. laevigatus was a shallow infaunal suspension feeder (e.g. Hautmann et al. 2013).

Superorder HETERODONTA Neumayr, 1884
Order VENEROIDA Adams and Adams, 1856
Superfamily LUCINOIDEA Fleming, 1828
Family LUCINIDAE Fleming, 1828

Genus SINBADIELLA Hautmann and Nützel, 2005

Sinbadiella pygmaea Hautmann and Nützel, 2005
Figure 13F

*2005 *Sinbadiella pygmaea* Hautmann and Nützel, p. 1133, pl. 1 figs. 1–20, Text-fig. 2.

Material. Rarely recorded in samples SR-2 and TO-A-1. The description is based on the well preserved specimen PIMUZ 30693.

Description. Shell equivalved, moderately inflated, subquadrate in outline, slightly longer than high. Anterior margin extended, posterior margin blunt. Umbones strongly prosogyrate and placed at about 40% of the dorsal margin. Lunule deep. Ornamentation and internal features not observed.

Discussion. This species is easily identified by its prosogyrate umbo and its deep lunule. The material found herein agrees well with the specimens from the Sinbad Formation figured in Hautmann and Nützel (2005)

Ecology. Having been assigned tentatively to the family Lucinidae, *S. pygmaea* was possibly a shallow-burrowing infaunal chemosymbiotic bivalve (Hautmann and Nützel 2005)

Family MACTROMYIDAE Cox, 1929

Genus UNICARDIUM d'Orbigny, 1850

Unicardium? sp. A
Figure 13H

Material. External mould of one left valve from sample DH-1-gs2.

Description. Valve well inflated, subelliptical in outline. Umbo wide, slightly prosogyrate, placed at the midst of dorsal margin.

Discussion. Generic identification is tentative due to the very few observable morphological criteria and the limited amount of material. However, the specimen is clearly distinguished by its broad umbo from other superficially similar forms such as the herein described species of Unionites. The external morphology is similar to Middle Triassic species assigned to *Unicardium* (e.g. *Unicardium schmidi* Geinitz 1842), in which it is provisionally placed.

Superfamily CRASSATELLOIDEA de Férussac, 1822
Family MYOPHORICARDIIDAE Chavan in Vokes, 1967

Genus SEMENTICONCHA Hautmann et al., 2013

Sementiconcha recuperator Hautmann et al., 2013
Figure 13G

* 2013 *Sementiconcha recuperator* Hautmann et al, p.284, fig. 8.A–L.

Material. One specimen from SR-4 (PIMUZ 30694).

Description. Shell equivalved, moderately inflated, with sharp diagonal carina. Outline of valves subrectangular, posteriorly truncated. Posterior dorsal margin straight. Beak located at anterior 30% of dorsal margin. Umbones prosogyrate. Lunule well

developed. Ornamentation and internal features not observed.

Discussion. Although only one specimen is available, species identification is possible on the basis of the well developed carina and the distinctly prosogyrate umbo. This species, originally described from the Spathian Virgin Formation (Hautmann et al. 2013), occurs there in high numbers in subtidal low energy deposits (Hautmann et al. 2013). The record in the Sinbad Formation reveals that this species was already present in Smithian of the western US.

Ecology. S. recuperator was a shallow burrowing suspension feeder (Hautmann et al. 2013)

Gastropods
by Richard Hofmann *and* Alexander Nützel

Class GASTROPODA Cuvier, 1795
Order VETIGASTROPODA Salvini-Plawen, 1980
Superfamily TROCHONEMATOIDEA Zittel, 1895
Family LOPHOSPIRIDAE Wenz 1938

Genus WORTHENIA De Koninck 1883

Remarks. The Palaeozoic genus *Worthenia* and the Triassic genus *Wortheniella* Schwardt 1992 closely resemble each other and are distinguished by the morphology of the early teleoconch. The early teleoconch of the few Early Triassic species assigned to *Worthenia* are unknown. Thus, these Early Triassic species are left in the previously suggested systematic position until better preserved material becomes available.

Worthenia windowblindensis Batten and Stokes, 1986
Figure 14A

*1986 *Worthenia windowblindensis* n. sp. Batten and Stokes, p. 6, figs. 1–3.
2005 *Worthenia windowblindensis* Nützel and Schulbert, p. 507, fig. 11H.

Material. One specimen recorded from sample DH-1-3 (PIMUZ 30704).

Description. Relatively low-spired shell with gradate whorl profile. Three whorls developed with well incised sutures. Ornamentation with at least three equidistant spiral chords with intercalated fine spiral threads. Upper whorl face with broad shallow ramp that is flat to slightly concave. Selenizone was probably situated at edge of ramp. Collabral ornament absent. First whorl and aperture not observed.

Remarks. W. windowblindensis is easily recognized by the missing collabral ornament which is otherwise characteristic for the genus (Batten and Stokes 1986). This species has been erected based on material from the Sinbad Formation (Batten and Stokes 1986) which represents a shallow marine equivalent of the occurrence studied herein.

Ecology. W. windoblindensis was an epifaunal detritus feeder.

Superfamily TURBINOIDEA Rafinesque, 1815
Family ATAPHRIDAE Cossmann 1915

Genus CHARTRONELLA Cossmann, 1902

Chartronella? sp. A
Figure 14B

Material. Recorded in very few numbers in the lower part of the Sinbad Formation from the samples TO-A-1, SR-1, SR-2, and SR-3. The description is based on specimen PIMUZ 30705.

Description. Turbiniform, relatively high-spired shell with deeply incised sutures. Whorls convex, somewhat angulated at or slightly above mid-whorl, moderately inflated with ramp.

Remarks. Given the poor preservation, identification of the material at hand is not unwarranted. The only genus reported from the Sinbad Formation by Batten and Stokes (1986) which agrees with the general shape and the presence of a subsutural ramp is *Chartronella*.

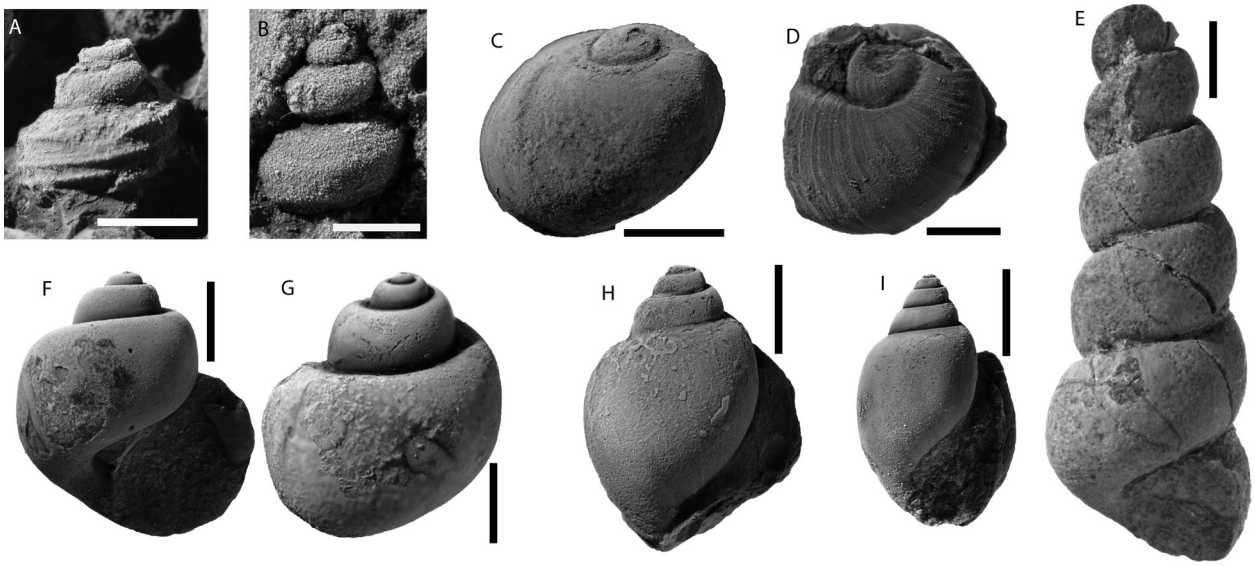

FIG. 14. A, *Worthenia windowblindensis*, sample DH-1-3, PIMUZ 30704, scale bar represents 2 mm B, *Chartronella* sp. A, sample SR-3, PIMUZ 30705, scale bar represents 2 mm. C, *Abrekopsis* cf. *depressispirus*, sample SR-3, PIMUZ 30706, scale bar represents 4 mm. D, *Neritaria costata*, sample, SR-4, PIMUZ 30707, scale bar represents 2 mm. E, *Polygyrina* sp. A, sample DH-1-gs2, PIMUZ 30708, scale bar represents 5 mm. F – G, *Laubopsis*? sp. A, sample DH-1-gs1, PIMUZ 30709, all scale bars represent 5 mm. F, apertural view. G, lateral view. H, *Strobeus batteni*, sample DH-1-gs-1, PIMUZ 30710, apertural view, scale bar represents 10 mm. I, *Strobeus batteni*, DH-1-gs-1, PIMUZ 30711, apertural view, scale bar represents 10 mm.

Ecology. C. sp. A is interpreted as an epifaunal detritus feeder.

Order NERITIMORPHA Koken, 1896
Superfamily NERITOPSOIDEA Gray, 1847 (= Rafinesque, 1815)
Family TRICOLNATICOPSIDAE Bandel 2007

Genus LAUBOPSIS Bandel, 2007

Laubopsis? sp. A
Figure 14F–G

Material. Very common in samples DH-1-gs-1 and DH-1-gs2. The description is based on abundant steinkerns from sample DH-1-gs2.

Description. Shell turbiniform, low-spired with convex inflated somewhat shouldered whorls. Last whorl much higher than spire. Suture deeply incised. Periphery of mature whorls flattened. Aperture subcircular, oblique, somewhat higher than wide. Base phaneromphalous, possibly with umbilical plug.

Remarks. The present material consists of numerous specimens, which form a distinct species in the collection from beds DH-1-gs1 and DH-1-gs2. However, based on steinkerns, it is almost impossible to determine this species properly. It shares the general shape, the phaneromphalous condition and the form of the aperture with the neritimorph genus *Laubopsis*, which was originally described from the Late Triassic Cassian Formation of the Dolomites (Bandel 2007). Some of the present specimens seem to have an umbilical plug which could also support a placement within neritimorphs. However, shells like this are also known from other gastropods such as naticids or certain vetigastropods.

Ecology. Epifaunal, probably grazers or detritus feeders.

Superfamily NERITOIDEA Rafinesque, 1815
Family NERITIDAE Rafinesque, 1815

Genus ABREKOPSIS Kaim, 2009

Abrekopsis cf. *depressispirus* (Batten and Stokes, 1986)
Figure 14C

cf. 1986 *Naticopsis depresispirus* n. sp., Batten and Stokes, p. 12, figs. 11 – 13.
cf. 2009 *Abrekopsis depressispirus*, Kaim, p. 150, fig. 140.

Material. Fairly abundant in samples SR-1, SR-2, MV-2, DV-3, otherwise recorded in smaller numbers in samples SR-3 and TO-A-1 to TO-A-6. The description is based on a well preserved specimen from sample SR-3 (PIMUZ 30706).

Description. Shell globose, egg-shaped, very low-spired. Whorls rounded, rapidly increasing, embracing most of the preceding whorls. Shallow suture. Faint prosocline growth lines.

Discussion. This form is probably conspecific with *Abrekopsis depressispirus* (Batten and Stokes 1986; Kaim 2009). However, since the aperture and the apex are not preserved in the present material, we prefer to present it in open nomenclature. This form is known from Early Triassic of the western US (Batten and Stokes 1986) and Far East Russia (Kaim 2009). Similar neritimorphs have repeatedly been documented from Early Triassic formations of various areas e.g. *Naticopsis* sp. from the Salt Range, Pakistan, *Naticopsis* from Oman (Kaim et al.2013; Wheeley and Twitchett 2005). Due to a low number of shell characters, their taxonomy is very difficult especially if the preservation is not excellent.

Family NERITARIIDAE Wenz, 1938
Subfamily NERITARIINAE Wenz, 1938

Genus NERITARIA Koken 1892

Neritaria costata Batten and Stokes, 1986
Figure 14D

*1986 *Neritaria costata* Batten and Stokes, p. 16, figs. 20, 21.

Material. Recorded with one specimen in sample SR-4 (PIMUZ 30707).

Description. Small depressed neritiform shell with rapidly expanding whorls and deeply incised suture. Ornamentation consists of prosocline, slightly prosocyrt axial ribs. First whorl and aperture not observed.

Remarks. This species was first described from the same locality by Batten and Stokes (1986), which is also the only locality from which is has thus far been reported. Neritimorphs with prominent axial ribs are not very diverse in the Early Triassic. Only '*Natiria*" *costata* is frequently observed in upper Werfen Formation of the Dolomites (Nützel 2005). Bandel (2007) erected two Late Triassic genera which have a prominent axial ornament: *Colubrellopsis* and *Ladinaticella. N. costata* may belong to one of these genera. However, the type species of *Neritaria* is entirely smooth.

Ecology. N. aequicostata was an epifaunal detritus feeder.

Order CAENOGASTROPODA Cox, 1960
Superfamily ACTEONINOIDEA Cossmann, 1895
Family SOLENISCIDAE Knight, 1931

Genus STROBEUS de Koninck, 1881

Strobeus batteni Kaim et al., 2013.
Figure 14H

1986 *Strobeus* cf. *paludinaeformis* (Hall); Batten and Stokes 1986: 29, figs: 49-51.
2005 *Soleniscus* sp. or *Strobeus* sp., Nützel 2005: 441, fig: 7 middle and right.
2005 *Soleniscus*?, Wheeley and Twitchett 2005: 40, fig. 2L, M.
2010 '?*Naticopsis*-?*Omphaloptycha*", Brayard et al., p. 148, figs 1 A, B.
2013 *Strobeus batteni*, Kaim et al. p. 6, figs 6C-E, I.

Material. Very common in samples DH-1-gs1, DH-1-gs2, and DH-1-9. The description is based on abundant steinkerns from the sample DH-1-gs2.

Description. Shell egg-shaped, varying from elongated to rather bulbous, low-spired with last whorl much higher than spire. Spire acutely conical. Whorls convex evenly rounded, embracing somewhat below suture. Suture distinct. Aperture tear drop-shaped, round anteriorly, acute posteriorly. Parietal lip convex. Columellar fold present but rarely visible. Aperture probably

with weak anterior canal. Growth lines more or less orthocline to slightly prosocyrt.

Remarks. The present material seems to be close to *Strobeus batteni* as described by Kaim et al. (2013) from the early Smithian of Pakistan. These authors also included material from the Sinbad Formation, which was described as *Strobeus* cf. *paludinaeformis* by Batten and Stokes. (1986). However, the assignment is somewhat tentative due to the steinkern preservation of the present material. There are broader, bulbous specimens (Fig. 14H) as well as somewhat more slender specimens (Fig. 14I) present in our collection. We interpret this as intraspecific variability although it is possible that two species are present.

Ecology. Epifaunal to semi-infaunal, detritus or sediment feeders, microcarnivory possible.

Family POLYGYRINIDAE Bandel 1993

Genus POLYGYRINA Koken, 1892

Poylgyrina sp. A
Figure 14E

?1986 *Coelostylina* sp. b, Batten and Stokes, p. 25, fig. 40.
2010 '*Polygyrina*', Brayard et al., p. 148, figs 1 C–H, 3.

Material. Rather rare in the samples TO-A-1, TO-A-2, SR-2, SR-3, DH-1-0, DH-1-gs2. Fairly abundant in the sample MV-2 and TO-A-2. The description is based on the comparatively large specimens from sample DH-1-gs2 (PIMUZ 30708)

Description. High-spired shell. Whorls smooth, convex, evenly inflated. Suture well incised and straight. Protoconch and aperture missing.

Remarks. Similar high-spired gastropods of the Early Triassic were traditionally assigned to the genus *Coelostylina*. However, most of the Early Triassic material assigned to *Coelostylina* is preserved as steinkerns and provides very few criteria to facilitate a precise genus and species identification. Accordingly, species tend to be lumped into poorly defined dustbin genera such as *Coelostylina* or *Polygyrina* (Nützel 2005). The same is true for the material of the Sinbad and the Thaynes Formation. The specimens observed in this study are very likely conspecific with '*Polgyrina*' reported in Brayard et al. (2010) from the same bed as the specimen figured herein but no systematic discussion accompanied that study. *Coelostylina* sp. b in Batten and Stokes (1986) from the Sinbad Limestone (San Rafael Swell) agrees well with our material and could be conspecific although it has a slightly larger apical angle. The Late Triassic type species of *Coelostylina* and *Omphaloptycha* are small to medium-sized shells which have a much lower spire than the present material i. e., the last whorl exceeds the spire height by far in both genera. Moreover, they have umbilical niches. The general shape of the present material is close to that of *Polygyrina lommeli* from the Late Triassic Cassian Formation where it is most abundant in autochthonous soft bottom communities or algal meadow assemblages (Fürsich and Wendt 1977). However, material with shell preservation is required for a precise taxonomic assignment.

Ecology. Polygyrina was an epifaunal detritus feeder.

Brachiopods

by Richard Hofmann

Phylum BRACHIOPODA Dumeril, 1806
Class LINGULATA Goryansky and Popov, 1985
Order LINGUILIDA Waagen, 1885
Family LINGULIDAE Menke, 1828

Genus LINGULARIA Biernat and Emig, 1993

Discussion. Lower Triassic lingulids were traditionally (e.g. Bittner 1899; Newell and Kummel 1942) but also in more recent studies (e.g. Rodland and Bottjer 2001, Hofmann et al. 2013b) placed in *Lingula*. Biernat and Emig (1993) pointed out that Palaeozoic and many Mesozoic '*Lingula*' show marked internal differences to extant species of the genus such as the shape of the posterior adductor muscle, the size of the lophophoral cavity, and shorter ventral vascular lateralia. The state of preservation in our material does not allow identification of these features with certainty. However, the conspicuous, relatively deep paired grooves (Fig. 15A) along the midline are joining at the posterior end of the shell are suggestive for *Lingularia* because they suggest the presence of a symmetrical heart-shaped adductor muscle scar diagnostic for this genus (Biernat and Emig 1993). In *Lingula*, this structure is reduced to one lateral scar which results in curved continuous pedicle grooves.

Lingularia borealis (Bittner, 1899)
Figure 15A

*1899 *Lingula borealis* nov. spec.; Bittner, p. 25, pl. 4, figs. 1–7.
1942 *Lingula borealis* Bittner; Newell and Kummel, p. 953, pl. 2, figs. 1–4.
?1993 *Lingularia similis* sp. n.; Biernat and Emig, p. 11, fig. 3.
2013 *Lingula borealis* Bittner; Hofmann et al., p. 868, fig. 8.24.

Material. Recorded from the samples DH-1-0, DH-1-1a, DH-1-3, DV-1, DV-2, DH-3-1.

Description. Shells elongate and oval in outline, lateral margins subparallel, posterior parts of both valves weakly inflated along median longitudinal line. Shell surface generally smooth except for concentric fine growth lines. Ventral valve with parallel pedicle ridge terminating towards the posterior part.

Discussion. The specimens from the Thaynes Group agree well with figures and the description of *'Lingula' borealis* (Bittner 1899; Newell and Kummel 1942), which has been included in the type species of *Lingularia* (*L. similis*) by Biernat and Emig (1993). This allocation remains dubious because it was based on the fact that Bittner (1899) did not provide descriptions of criteria considered as diagnostic by Biernat and Emig (1993). This might be unfortunate but does not justify priority of their new species *L. similis*. If Bittner's material turns to out share the same diagnostic characteristics with *L. similis, Lingularia borealis* would be the older and thus valid synonym (see also Holmer and Bengtson 2009). In our view, *Lingularia borealis* is, thus, a valid species and the figures provided by Bittner (1899) and Kummel and Newell (1942) allow a precise allocation of our material. Peng and Shi (2008) erected the new species *Sinolingularia huananensis*, which is very similar to *Lingularia borealis*. This has been also noted by Peng and Shi (2008) who tentatively assigned "some […] Early Triassic *Lingula borealis* into the new species *Sinolingularia huananensis.* However, without a proper synonymy list, it remains unclear which published *Lingula borealis*' were assigned to S. huanan-

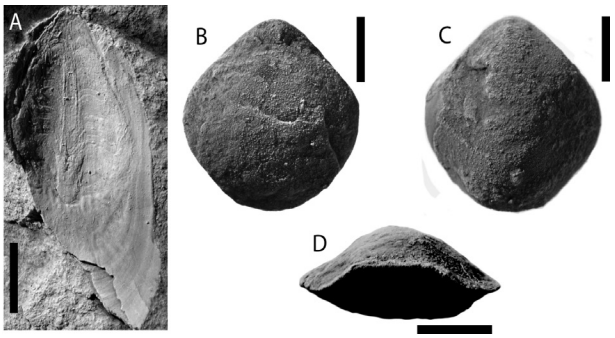

FIG. 15. A, *Lingularia borealis*, sample DV-1, ventral valve, PIMUZ 30701. B–D, *Obnixia thaynesiana*, sample CP-102. B, dorsal view, PIMUZ 30703. C, ventral view, PIMUZ 30703. D, Anterior view, PIMUZ 30702. All scale bars represent 3 mm.

ensis. According to Peng and Shi (2009), the diagnostic differences between *Lingularia* and *Sinolingularia* are the presence of separated dorsal antero-lateral muscle scars and posteriorly extended pedicle grooves in the ventral valve. Our material does not allow a clear differentiation because the dorsal valves are too poorly preserved. However, because Biernat and Emig (1993) noted the close morphological similarity of the specimens of Newell and Kummel (1942) to L. similis, we prefer to include our material in *Lingularia*.

Lingularia borealis has been frequently reported from the Panthalassa margin (Bittner 1899; Rodland and Bottjer 2001; Shigeta et al.; 2009). The prolific appearance of *Lingularia* in the aftermath of the end-Permian mass extinction has been linked to particular ecological conditions, environmental stress or a combination of both factors (Rodland and Bottjer 2001). *Lingularia* is particularly abundant in the Griesbachian to Dienerian Dinwoody Formation (Rodland and Bottjer 2001). Our studies (Hofmann et al. 2013a) suggest that the wide occurrence of *Lingularia borealis* may be attributed to a combination facies effects and ecospace vacation, which enables eurytopic taxa such as Lingularia to thrive in habitats which are inhabited by more specialized taxa during background times. Observations in the Dinwoody Formation indicate that *Lingularia borealis* becomes rare or absent as soon as other taxa became established in benthic communities. This supports the hypothesis that the proliferation of *Lingularia* seems, besides certain facies effects, a real phenomenon which is attributed to a preceding extinction event. With respect to this consideration, it is interesting to note that *Lingularia borealis* is exclusively recorded in lower Smithian strata in the investigated area, which could indicate that benthic ecosystems may have been affected by faunal decimation just before the initial Thaynes transgression.

Class RHYNCHONELLATA Williams et al. 1996
Order TEREBRATULIDA Waagen 1883
Suborder TEREBRATULIDINA Waagen, 1883
Superfamily CRYPTONELLOIDEA Thomson, 1926
Family CRYPTONELLIDAE Thomson, 1926
Subfamily CRYPTACANTHIINAE Stehli, 1965

Genus OBNIXIA Hoover, 1979

Obnixia thaynesiana (Girty, 1927)
Figures 15B–D

*1927 *Terebratula thaynesiana* n. sp., Girty, p. 435, pl. 30, figs. 8–11.
?1979 *Protogusarella smithi* n. sp. Perry and Chatterton, p. 317, pl. 2, figs. 1–32, text-figs. 4–6.
1979 *Obnixia thaynesiana* (Girty, 1927), Hoover, p. 12, pl. 2 figs. 8–27, pl. 3 figs. 1–13.

Material. This species is exclusively record in sample CP-102. The description is based on the well preserved specimens PIMUZ 30703 and 30702.

Description. Shell rounded-subpentagonal, length and width being subequal. Ventral valve notably more convex than dorsal valve. Apex suberect. Commissure wide-uniplicate. Surface smooth.

Remarks. This species is exclusively observed from the Early Triassic of the western US (Hoover 1979). Very few terebratulide brachiopod species, on which Hoover (1979) gave a systematic overview, are known from the Early Triassic of the western US. The material observed herein agrees very well with the features and figures of *Obnixia thaynesiana*, which was originally introduced as *Terebratula thaynesiana* by Girty (1927) Although the internal morphology has not been figured in Girty (1927), we follow Hoover (1979) in suggesting that the material of Girty (1927) is conspecific with his specimens. A very similar form, *Protogusarella smithi*, was erected by Perry and Chatterton (1979). This species probably differs from *T. thaynesiana* in being more equiconvex, having a weaker ventral fold, possessing a dorsal sulcus, and lacking a medial plication. However, Girty (1927) noted that his *T. thaynesiana* is morphological highly variable. Unfortunately, he did not figure internal features, which are important for a correct identification. The internal features figured by Hoover (1979) refer to the paralectotype and, thus, it cannot be excluded that P*rotogusarella smithi* and *Obnixia thaynesiana* (sensu Girty 1927) are conspecific. If this is the case (i) *Protogusarella smithi* is an obsolete species, and (ii) *Obnixia* takes priority over *Protogusarella* or vice versa. Both genera were erected in 1979 and it has to be worked out, which one was published earlier.

Ecology. O. thaynesiana was a pedunculate epifaunal suspension feeder.

PALAEOECOLOGY OF THE THAYNES GROUP AND SINBAD FORMATION

In the Smithian part of the Thaynes Group and Sinbad Formation, the most dominant benthic guilds (*sensu* Aberhan 1994) are shallow infaunal, epibyssate and endobyssate epifaunal (bivalves) suspension feeders as well as epifaunal grazers (gastropods). The gastropod *Strobeus*, which is locally abundant, probably represents an epi- to semi-infaunal carnivore. Free lying suspension feeders (*Pernopecten*) are also present but rare. *Sinbadiella pygmaea* was possibly an infaunal chemosymbionthic lucinid bivalve (Hautmann and Nützel 2005). Although not recognized in this study, sponges as cementing suspension feeders became definitely established by Smithian times in the western US (Brayard et al. 2011). Ophiuroids and asteroids, which are epifaunal carnivores or detritus feeders, were very rarely observed and were not recognized in samples contributing to the associations studied herein. However, micro facies analysis that is currently carried out (Vennin et al. ongoing work) demonstrates that they may be extremely abundant in thin sections. This adds up to nine out of 13 typically Mesozoic benthic guilds (Aberhan 1994). The ecological spectrum of the Spathian part of the Thaynes Formation (sections MV and CP) is the same with the only exception that crinoids and articulate brachiopods are locally abundant. Brachiopods, are absent before the Spath-

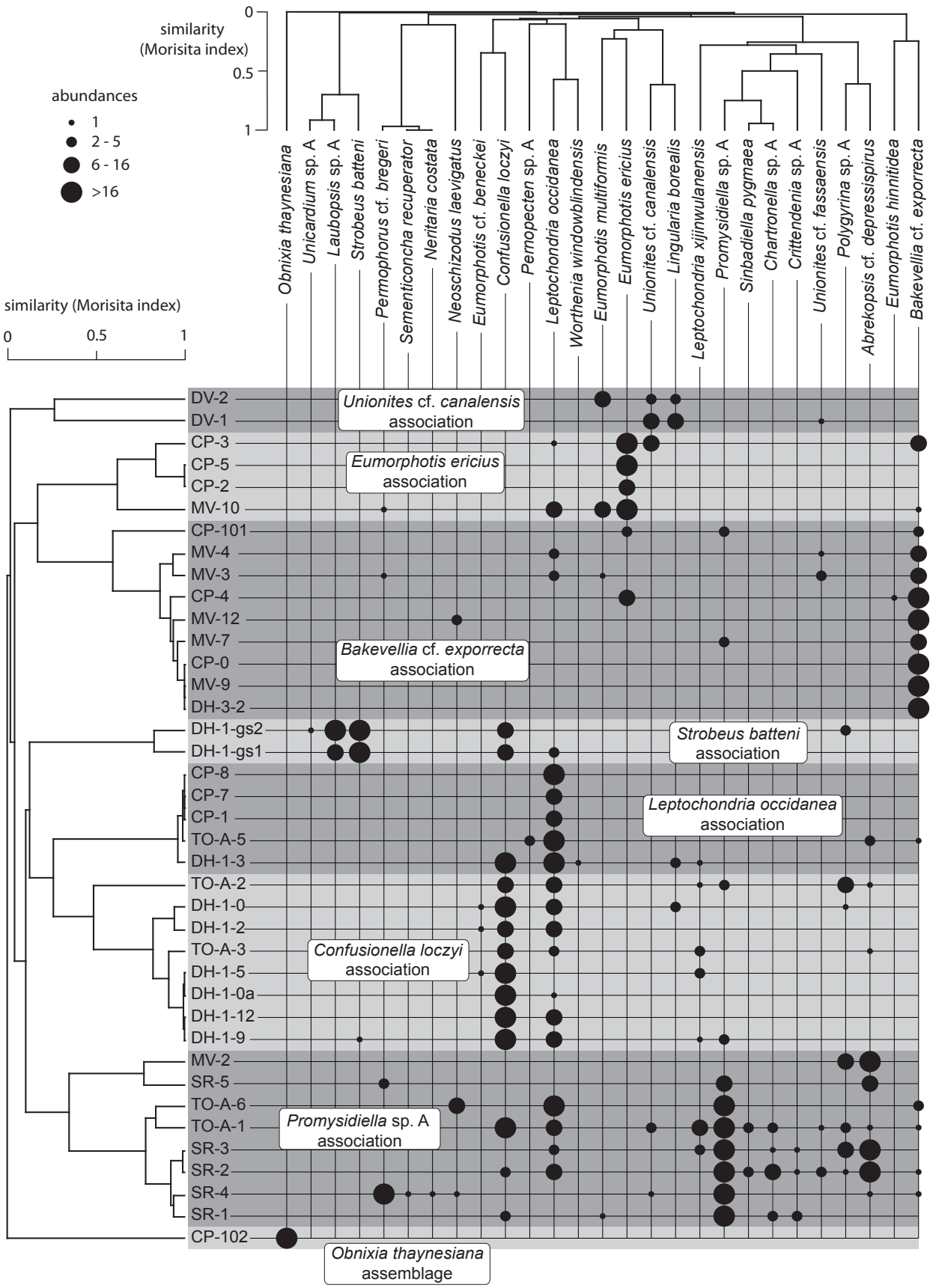

FIG. 16. Q-mode (samples) and R-mode (species) cluster analysis using the unweighted paired group algorithm and Morisita index of similarity. Classes of abundances (circle size) represent the quartiles of absolute abundance frequencies.

ian in the investigated sections.

Faunal associations and assemblages are obtained by Q-mode cluster analysis (Fig. 16), which groups individual samples based on the occurrence and abundance of taxa within the data set. Seven associations and one assemblage (*sensu* Fürsich 1984) were recognized in the Thaynes Group and the Sinbad Formation. These are characterized in the following paragraphs.

Unionites *cf.* canalensis *association*. This association (Fig. 17A) is represented by samples DV-1 and DV-2.The trophic nucleus comprises the species *Unionites* cf. *canalensis*, *Lingularia borealis* and *Eumorphotis mutliformis*. Also recorded is the infaunal suspension feeding bivalve *Unionites* cf. *fassaensis*. Species richness is 3 in both samples. Dominance is moderate with D values ranging from 0.52–0.55. The ecological spectrum comprises epifaunal and infaunal suspension feeders. The rarefaction curve indicates that further sampling would not have significantly increased alpha diversity of this association. Although the low number of samples and specimens impedes reliable statements, this association shows a very low alpha and guild diversity, and it is confined to the lowermost Smithian interval of the investigated area.

Eumorphotis ericius *association*. This association (Fig. 17B) comprises samples CP-2, CP-3, CP-5 and MV-10. The trophic nucleus involves *Eumorphotis ericius* and *E. mutliformis*. The

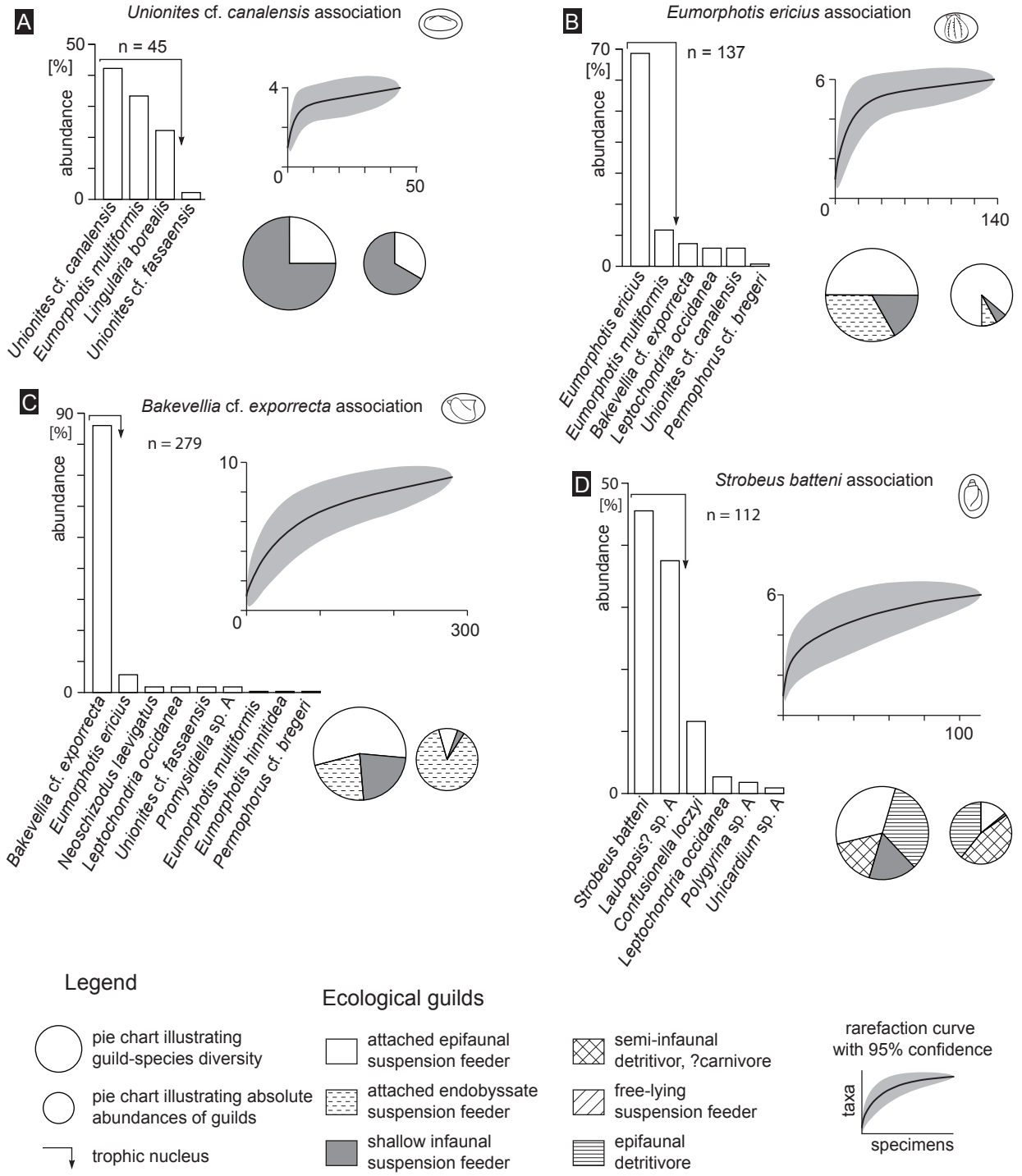

FIG. 17. Features of the benthic association of the Thaynes Group and Sinbad Formation. A, *Unionites* cf. *canalensis* association. B, *Eumorphotis ericius* association. C, *Bakevellia* cf. *exporrecta* association. D, *Strobeus batteni* association.

remaining species are *Bakevellia* cf. *exporrecta, Leptochondria occidanea, Unionites* cf. *canalensis* and *Permophorus* cf. *bregeri*. Sample species richness ranges from 1–5 (mean 2.75). Dominance ranges from 0.33–1 (mean 0.69). Guild diversity is 3 with epifaunal suspension feeding bivalves representing the main constituents. Semi-infaunal and infaunal bivalves play only a minor role, especially in terms of absolute abundance of guilds. The rarefaction curve indicates that the overall diversity of 6 species approximates expected diversity. The *E. ericius* association is most notably recorded in strata which are lower Spathian in age. Abundant occurrences of large *E. ericius* and *E. multiformis* which form thick-bedded bioclastic limestones were observed in all sections exposing strata of this time interval, which suggests that these species experienced a rapid expansion, at least in mid and inner shelf habitats.

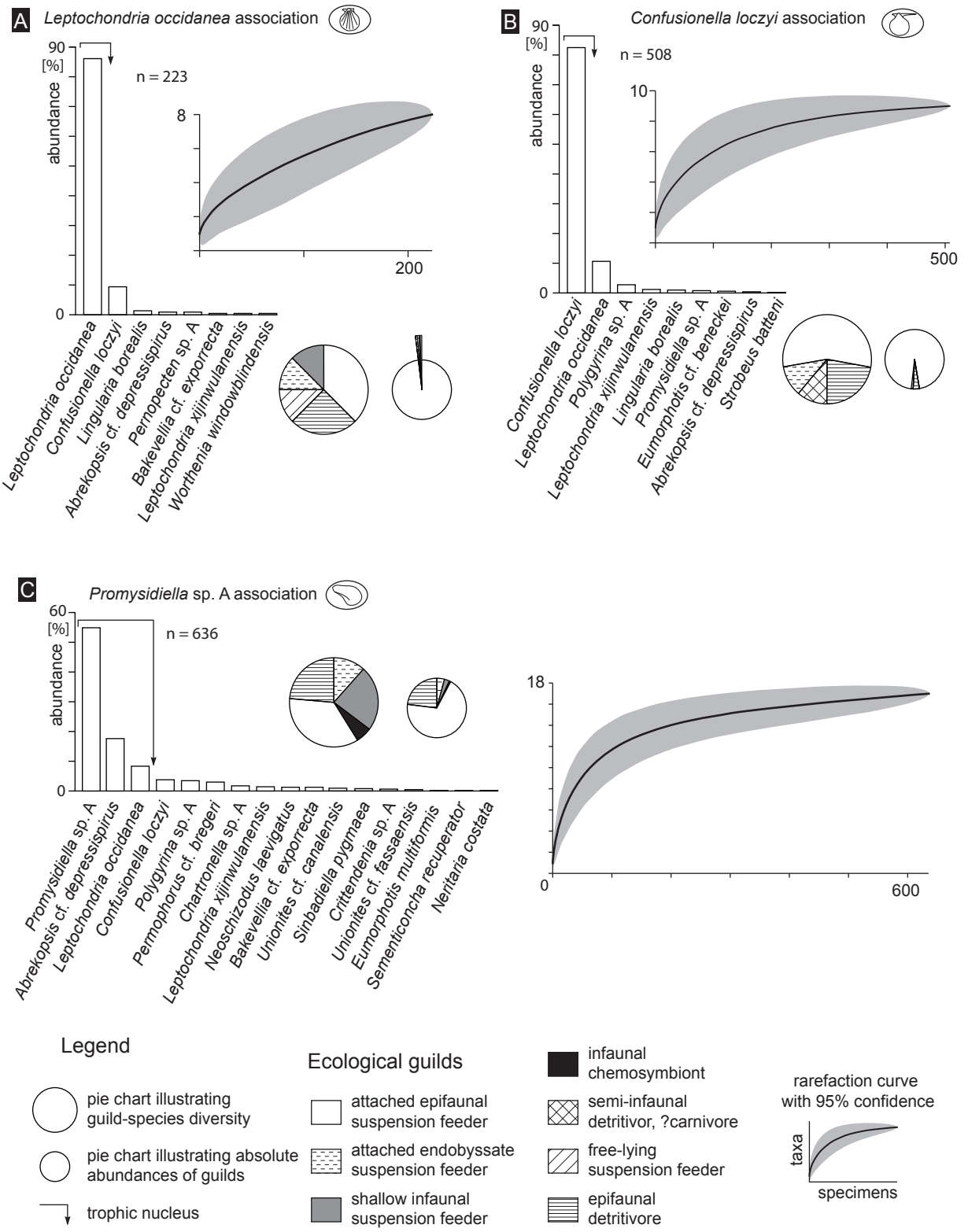

FIG. 18. Features of the benthic association of the Thaynes Group and Sinbad Formation. A, *Leptochnodria occidanea* association. B, *Confusionella loczyi* association. C, *Promysidiella* sp. A association.

Bakevellia *cf.* exporrecta *association*. This association (Fig. 17C) is represented by samples CP-101, MV-4, MV-3, CP-4, MV-12, MV-7, CP-0, MV-9, and MV-3-2. *Bakevellia* cf. *exporrecta* constitutes its trophic nucleus. All other species (*Eumorphotis ericius, Eumorphotis multiformis, Eumorphotis hinnitidea, Leptochondria occidanea, Neoschizodus laevigatus, Unionites* cf. *fassaensis, Promysidiella* sp. A*, Permophorus* cf. *bregeri*) are recorded in very small numbers. Sample diversity ranges from 1–5 (mean 2.3). Dominance values range from 0.34–1 (mean 0.69). Guild diversity is 3 with epifaunal, semi-infaunal and infaunal suspension feeding bivalves recorded. Epifaunal bivalves dominate in terms of species per guild whereas semi-infaunal bivalves clearly dominate in terms of abundance. The rarefaction curve indicates that the merged diversity of 9 species is slightly lower than expected diversity. This association is limited to the lowermost Spathian in all sections where strata of this time interval are exposed.

Strobeus batteni *association*. The *Strobeus batteni* association (Fig. 17D) comprises samples DH-1-gs1 and gDH-1-s2. The trophic nucleus includes *Strobeus batteni* and *Laubopsis*? sp. A. *Confusionella loczyi* may be abundant. All other species (*Leptochondria occidanea, Polygyrina* sp. A, and *Unicardium* sp. A) are rare. Sample diversity is 4–5 (mean 4.5) and dominance is 0.39–0.41 (mean 0.4). The trophic guild diversity is 4 with epifaunal grazers, carnivores, and suspension feeders as well as infaunal suspension feeders that are balanced in terms of species per guild. In absolute abundances, infaunal suspension feeders are merely an accessory element. The overall diversity of 6 taxa seems to reflect the actual diversity as indicated by the rarefaction curve. This association is confined to an interval of the section DH-1 which exposes shales intercalated with thin limestone beds.

Leptochondria occidanea *association*. This association (Fig. 18A) is represented by samples CP-8, CP-7, CP-1, TO-A-5, and DH-1-3. The trophic nucleus is formed by *Leptochondria occidanea*. The secondmost common species is *Confusionella loczyi*. All other species (*Lingularia borealis, Abrekopsis* cf. *depressispirus, Pernopecten* sp. A, *Bakevellia* cf. *exporrecta, Leptochondria xijinwulanensis,* and *Worthenia windowblindensis*) are very rare. Sample diversity ranges from 1–5 (mean 2.4) and dominance values range from: 0.66–1 (mean 0.89). Trophic guild diversity is 5, with free lying, epifaunal, semi-infaunal, and infaunal suspension feeders as well as epifaunal grazers. Whereas the species per guild spectrum is balanced, the absolute abundance pattern shows that epifaunal suspension feeding bivalves are overwhelmingly dominant in this association. The overall diversity of 8 taxa slightly underestimates the expected diversity as indicated by the rarefaction curve. The L. occidanea association occurs in both inner and outer shelf settings and is not confined to a certain stratigraphic level.

Confusionella loczyi *association*. This associaton (Fig. 18B) is recorded by samples TO-A-2, DH-1-0, DH-1-2, TO-A-3, DH-1-5, DH-1-0a, DH-1-12, and DH-1-9. The trophic nucleus is represented by *Confusionella loczyi*. Also recorded but not particular abundant are the species *Leptochondria occidanea* and *Polygyrina* sp. A. Accessory elements are the species *Leptochondria xijinwulanensis, Lingularia borealis, Promysidiella* sp. A, *Eumorphotis* cf. *beneckei, Abrekopsis* cf. *depressispirus,* and *Strobeus batteni*. Diversity ranges from 2–6 (mean 3.6). Dominance values range from 0.28–0.94 (mean 0.57). Trophic guild diversity is 4, with epifaunal and semi-infaunal suspension feeders being present in addition to epifaunal grazers and carnivores. Species guild diversity is balanced but the epifaunal suspension feeders form the numerically dominating group. The well leveled rarefaction curve indicates that the overall diversity of 9 species in this association is close to the expected diversity. The C. loczyi association is predominantly recorded in outer shelf settings of section DH-1 and to far lesser extent in section TO-A.

Promysidiella sp. A *association*. This association (Fig. 18C) is recorded by samples: SR-1, SR-2, SR-3, SR-4, SR-5, MV-2, TO-A-6, and TO-A-1. The trophic nucleus is represented by the species *Promysidiella* sp. A, *Abrekopsis* cf. *depressispirus,* and *Leptochondria occidanea*. Minor elements are *Confusionella loczyi, Polygyrina* sp. A, and *Permophorus* cf. *bregeri*. The remaining species are very rare (*Chartronella* sp. A, *Leptochondria xijinwulanensis, Neoschizodus laevigatus, Bakevellia* cf. *exporrecta, Unionites* cf. *canalensis, Sinbadiella pygmaea, Crittendenia* sp. A, *Unionites* cf. *fassaensis, Eumorphotis multiformis, Sementiconcha recuperator, Neritaria costata*). Sample diversity ranges from 2–10 (mean 6.1) and dominance values range from 0.24–0.67 (mean 0.47). Trophic guild diversity is 4 and involves epifaunal, semi-infaunal, and infaunal suspension feeders, as well as epifaunal grazers. The species per guild diversity is quite balanced whereas in terms of absolute abundance, epifaunal bivalves are clearly dominating. The well leveled rarefaction curve suggests that the overall diversity of 17 species matches the expected diversity of this association. This association is largely confined to inner shelf habitats of the Sinbad Formation.

SPATIAL AND TEMPORAL TRENDS

The most notable pattern (Fig. 19) shown by the Smithian data is a distinction between inner and outer shelf communities with some overlap seen in mid-shelf settings. The Promysidiella sp. A association is exclusively found in strata deposited above the storm wave base. The Confusionella loczyi association, the Strobeus batteni and the Leptochondria occidanea associations predominate in outer- and mid shelf settings of the Confusion Range. The Unionites cf. canalensis association, found exclusively in the basal part of the section at Dog Valley, is recorded just above the oldest ammonoid beds (early Smithian) observed in the area, which could indicate a stratigraphic signal. Section DH-1 contains beds rich in benthic fauna from late early to latest Smithian. Faunal composition does not change over the recorded time span. The interfingering of the Confusionella loczyi, Strobeus batteni and Leptochondria occidanea associations is most likely related to proximal-distal trends. The Strobeus batteni association is restricted to rhythmic fine scale interbeddings of marly shales and limestones, which points to a more proximal position in an upper mid-shelf position. The other two associations are exclusively recorded in pack and grain stones that occur within barren shale intervals, are typical of mid- and outer shelf settings. Benthic communities were thus not affected by significant turnovers during the Smithian

Beds of Spathian age indicate a remarkable shift in faunal composition. As observed in all settings, there is a shift from typical Smithian association (see above) to associations that are dominated by Bakevellia cf. exporrecta and Eumorphotis ericius. The latter seems to be more common in thick bioclastic limestones deposited in mid and inner shelf facies. In the early Spathian, outer shelf deposits again contain the Leptochondria occidanea association.

In conjunction with the distribution of the associations (Fig. 19), some trends in alpha diversity (or sample richness per association) and dominance can be deduced with respect to facies (Fig. 20) and time (stratigraphic age). The Pro-

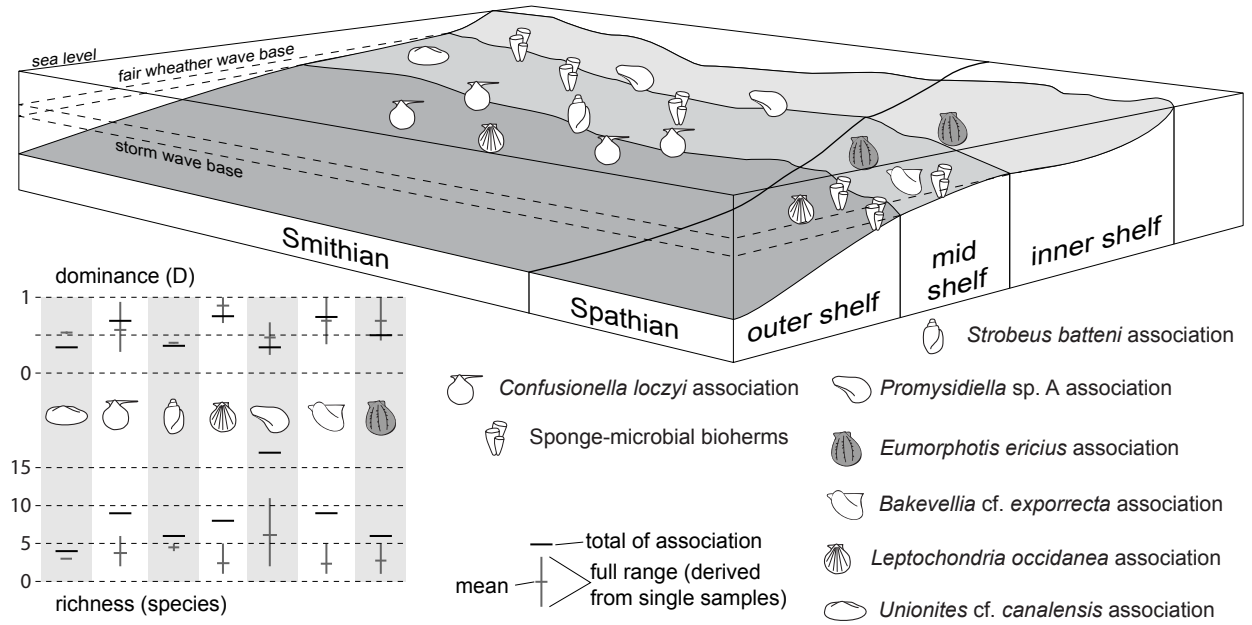

FIG. 19. General distribution of benthic associations associations from Smithian to Spathian in inner to outer shelf settings.

mysidiella sp. A association, which is predominantly observed in inner shelf settings, exhibits the highest mean and bulk diversity. All other associations have a much lower range of sample richness, a lower mean and overall diversity. The exceedingly higher overall diversity of the Promysidiella sp. A association may partly indicate some mixing of communities in the more heterogeneous inner shelf habitats. However, the fact that its species composition is relatively well reproduced in several samples (see Fig. 16) suggests that this effect is of minor importance. The Eumorphotis ericius assemblage dominates in lower Spathian inner shelf environments and is characterized by much lower diversity values. The Bakevellia cf. exporrecta association, which is predominantly recorded in Spathian outer shelf settings, also exhibits a low species diversity and high dominance value.

Trends in dominance values seem to be indistinct. Samples with high and low dominance values are essentially present over the whole stratigraphic and spatial range (Fig.20). The only notable pattern is that dominance increases in lowermost Spathian samples when compared to samples from the Smithian (Fig. 20).

DISCUSSION

Earlier studies (e.g.; Schubert and Bottjer 1995) suggested that recovery in benthic ecosystems did not start before the last stage of the Early Triassic (Twitchett and Wignall 1996) and that full recovery did not occur before the Middle Triassic (Schubert and Bottjer 1995). However, there is now a growing body of evidence for at least incipient benthic recovery during the Early Triassic (Krystyn et al. 2003; Shigeta et al. 2009; Kaim et al. 2010; Hautmann et al. 2011, 2013; Hofmann et al. 2011; Brayard et al. 2011). In combination with previous studies on the Early Triassic of the western US (Hofmann et al. 2013a, b), new data presented herein enable a comprehensive re-evaluation of the benthic recovery at the eastern margin of the tropical Panthalassa ocean. We outline and discuss below these data with respect to possible controls by intrinsic and extrinsic factors.

The early aftermath of the end-Permian mass extinction. Hofmann et al. (2013a) documented relatively diverse communities around the Griesbachian–Dienerian boundary in shallow marine habitats of the Dinwoody Formation, in accordance with observations of the same time interval in other regions such as Far East Russia (Shigeta et al. 2009), western (Krystyn et al. 2003; Hofmann et al. 2011) and eastern Tethys (Hautmann et al. 2011). This observation implies a relatively fast recovery during the Griesbachian, given the low richness and high dominance of faunas from the early Griesbachian. Communities of outer shelf settings have a poor record in the Dinwoody Formation and, where present, are mostly low in richness and high in dominance. This pattern could reflect harsh environmental conditions such as oxygen deficiency (Wignall and Hallam 1992) in the more distal settings or alternatively an onshore-offshore trend, with higher richness in more proximal settings (Miller 1988; Jablonski et al. 1983; Bottjer et al. 1996), poor preservation and record or a combination of each of these factors.

A Dienerian crisis? The upper part of the Dinwoody Formation is poorly constrained in terms of biostratigraphy. The presence of the bivalve species *Claraia mulleri* and *Claraia stachei*, which were recently correlated with ammonoid data (Ware et al. 2011), suggest an age close to the Griesbachian–Dienerian boundary. Strata above this interval remain biostratigraphically unresolved and the biostratigraphic context of the probable diachronous retreat of marine sedimentation in the Dinwoody basin is virtually unknown. Despite these uncertainties, strata above the last occurrence of *Claraia mulleri* and thus of a Dienerian age, show a significant decline back to simple benthic communities in the Gros Ventre Canyon section (Hofmann et al. 2013a). Data from Far East Russia (Shigeta et al. 2009) show the same trend with the highest benthic diversity observed in the upper Griesbachian and the lower Dienerian, and a subsequent drop before a new diversification at the base of the Smithian. The significance of this signal in the western US is unknown, but an overall review of species ranges in the Early Triassic of the western US indicates a notable turnover between post-Griesbachian and pre-Smithian strata in the western US, with 13 out of 19 species disappearing (Fig. 21). Four of these species became extinct on a global scale.

Some support for deleterious environmental conditions during the Dienerian is provided by environmental data. Ware et al. (2011) showed that anoxic conditions in open oceanic settings of Eastern Panthalassa were confined to the Dienerian. The same environmental signal has been shown by means

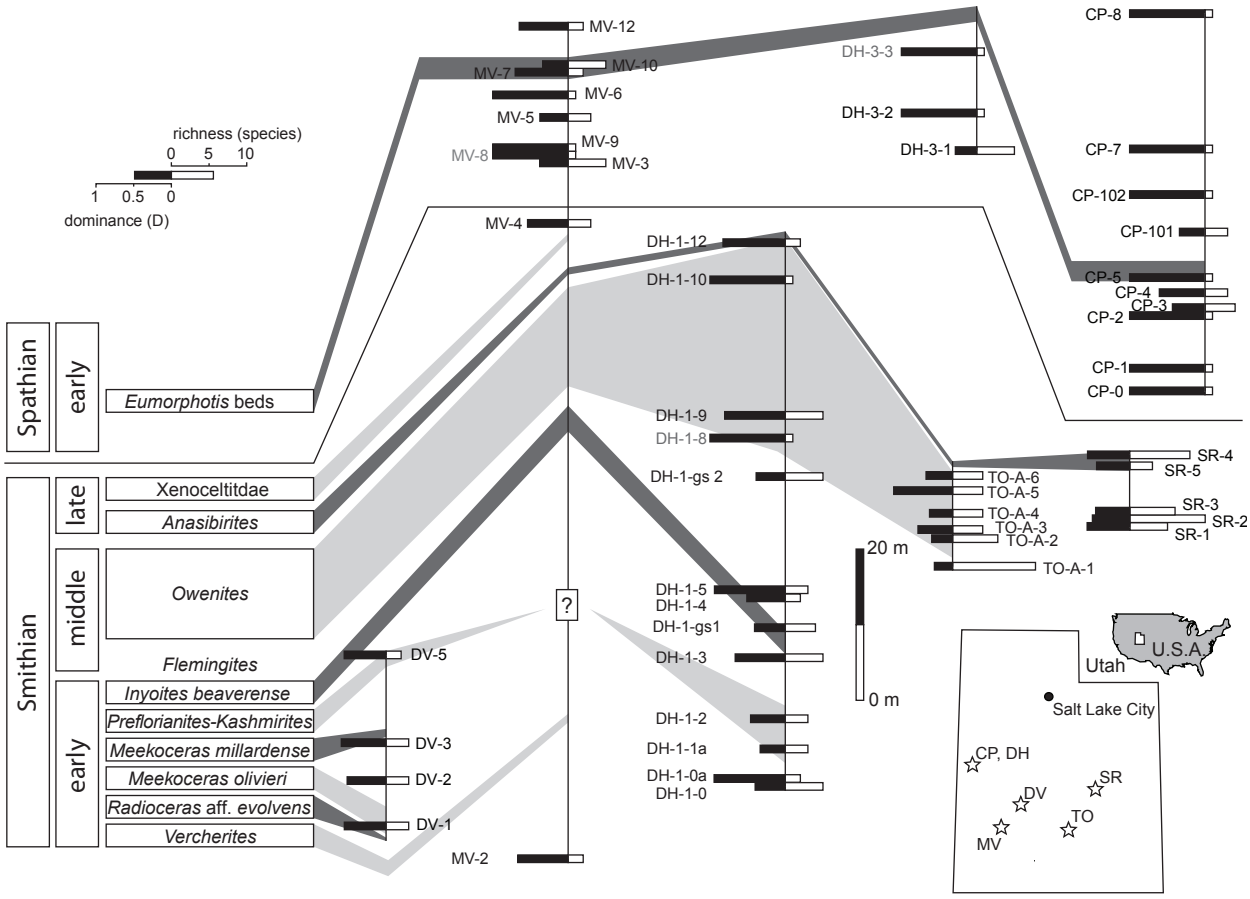

FIG. 20. Stratigraphic distribution of individual sample diversity (species richness) and dominance (Simpson D) in the study area; stratigraphic correlations are based on ammonoids.

of geochemistry for mid-latitude settings of eastern Panthalassa (Grasby et al. 2012). Palynofacies analysis confirms oxygen-restricted conditions for equatorial Tethyan successions of the Salt Range (Hermann et al. 2011). A further hint of at least local environmental deterioration is indicated by the proliferation of the disaster brachiopod genus *Lingularia*, which may be locally abundant in stressed habitats or becomes widespread in normal marine habitats by expanding into vacant ecospace after large defaunation events (Rodland and Bottjer 2001). Although *Lingularia* occurs throughout the Dinwoody Formation, it clearly dominates in the immediate aftermath of the extinction, but retreats in younger communities (Hofmann et al. 2013a), with exception of a short resurgence in the early Smithian of the study area. In all but these two time intervals of the Early Triassic, *Lingularia* is absent or very rare in the western US. This pattern seems to support the hypothesis that environmental conditions deteriorated during or before the lowermost Smithian.

In summary, a comparison between the Dinwoody Formation and the Thaynes Group in combination with data from other regions suggests that the Dienerian was likely a time of crisis for benthic communities, although direct information is absent due to the lack of marine strata in the western US.

The Smithian. Data presented in this paper show that faunas were ecologically and taxonomically relatively stable throughout the Smithian substage. Correlation of the benthic associations with the ammonoid zonation (Figs. 19, 20) indicates that variations in diversity, dominance, ecological and taxonomic composition are independent of their chronostratigraphic context. The only discernible trend is observed in the spatial distribution of communities. More diverse and balanced assemblages are confined to inner and mid shelf habitats of the Sinbad Formation. Accordingly, an onshore-offshore diversity trend, which is already seen in the Dinwoody Formation (Hofmann et al. 2013a), continues in the Thaynes Group and the Sinbad Formation. The mean alpha diversity as well as overall diversity of the Smithian associations is higher than in the Griesbachian and the Dienerian. The stratigraphic range of species (Fig. 21) shows that this rise is related to the establishment of species (18 out of 24) that were not recorded in the Dinwoody Formation. It is unlikely that all of these species evolved in the course of Smithian in this area. We therefore assume that the transgression during the early Smithian produced a more open marine shelf setting in comparison to the Dinwoody Formation, which promoted immigration of species, as previously suggested by Schubert and Bottjer (1995). This observation is further supported by the fact that ammonoids were virtually absent in the study area until the Smithian.

The late Smithian witnessed a dramatic and global decline in ammonoid diversity, which is also well documented in rocks in the western US (Brayard et al. 2009). Romano et al. (2013) recently demonstrated that this crisis is associated with large-scale fluctuations in the oxygen isotope record, which indicates dramatic climatic change across the Smithian substage. These fluctuations ranged from presumably temperate conditions during the early Smithian, hot conditions during the middle Smithian, and dramatic cooling during the late Smithian. Evidence for a benthic crisis is scarce. On a global scale, bellerophontoid gastropods became virtually extinct during the Smithian. They were diverse and globally distributed in Lower Triassic formations prior to the Spathian (Kaim and Nützel 2011). Only one younger occurrence of the bellerophontoid *Dicellonema* is reported from the Anisian of Tibet (Yü 1975) but remains controversial (see Kaim et al. 2013 for discussion).

However, in the data from the Thaynes Group there is no indication that the nekton crisis had an equivalent in benthic ecosystems. Samples from the ammonoid extinction interval (i.e. the *Anasibirites* Zone) are not notably different in taxonomic composition, ecological structure, diversity or dominance (Fig. 20). To test if benthic ecosystems suffered from any type of stress during the terminal Smithian, a comparison with samples from the Spathian is necessary.

A Smithian-Spathian boundary event? Examined strata occur notably below the oldest Spathian ammonoid zone recognized by Guex et al. (2010) and above the youngest Smithian ammonoid zone. As noted earlier, this time interval documents a remarkable shift in the composition of dominant species in benthic faunas of the western US. Fine-grained intervals typically host the *Bakevellia* cf. *exporrecta* association while bioclastic limestones record the *Eumorphotis ericius* association. This signal is accompanied by a drop in diversity and a rise in dominance of faunas (Fig. 20), possibly resulting from transient environmental changes. This shift is significant (Mann Whitney U test p-values < 0.05, performed with PAST and R) for the diversities from all Smithian and all Spathian samples, even if more diverse samples from the Sinbad Formation are excluded from the data set. The same is true for the dominance values but not if the samples of the Sinbad Formation are excluded (p= 0.11).

The bloom of the *Eumorphotis ericius* association is observed in all sections described. We herein refer to this bloom as the '*Eumorphotis* bioevent', which may be of stratigraphic value for intrabasinal correlations. In contrast to the Dienerian–Smithian transition (see above), there is however, no genus that actually went extinct at the Smithian-Spathian boundary. The shift in taxonomic composition of the benthic associations is not predominantly generated by the origination or immigration of new taxa, but by the increasing abundance of previously rare species. The majority of species that apparently disappeared in the lowermost Spathian belongs to newly evolved or range-through lineages that have a rich record later in the Triassic. Despite high dominance values and reduced species richness, there is thus no evidence for extinction of benthic taxa during this time interval.

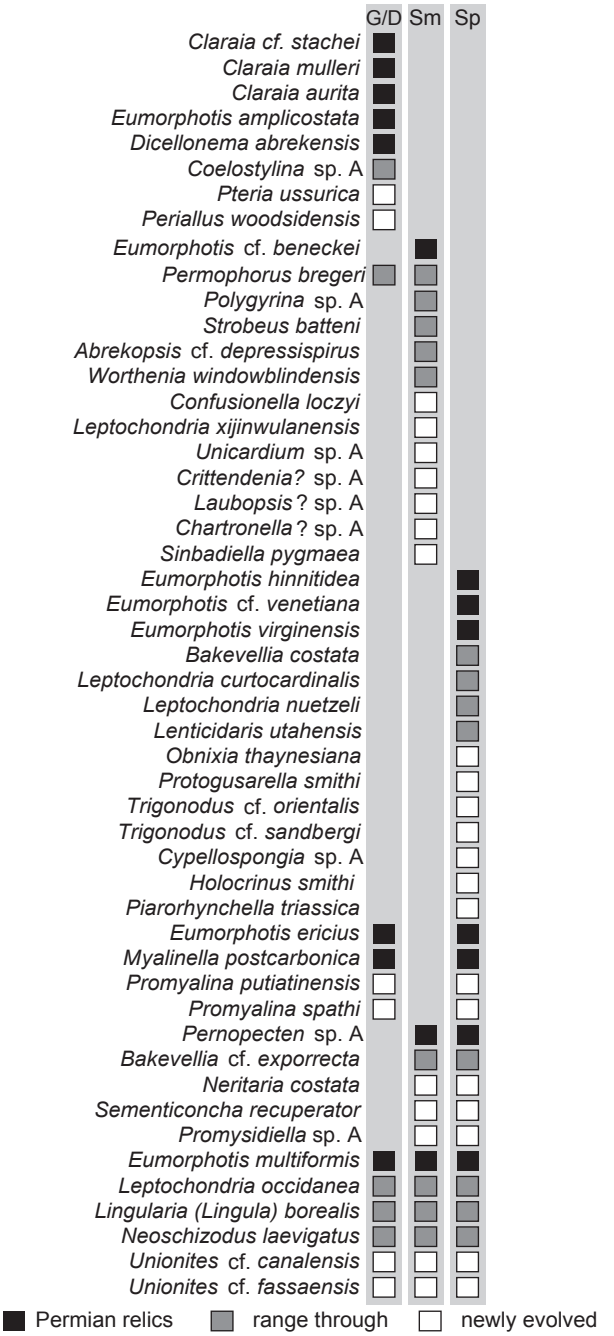

FIG. 21. Stratigraphic range of species reported by Hofmann et al. (2013a,b) and this work. G/D – Griesbachian-Dienerian, Sm – Smithian, Sp – Spathian.

The Spathian. Data from the late early Spathian Virgin Formation indicate that richness and ecological diversity of benthic faunas significantly increased in comparison to the Smithian. This is reflected by the high alpha diversity, high guild diversity and the generally more diverse ecological spectrum (Hofmann et al. 2013b) as well as by the high overall diversity (Hautmann et al. 2013). In terms of diversity and guild structure, the Virgin Fauna is actually more similar to Anisian benthic faunas than to any pre-Spathian fauna (McGowan et al. 2009; Hofmann et al. 2013b). Contrary to previous reports (e.g. Pruss and Bottjer 2004; Mata and Bottjer 2011), recent geochemical and palaeoecological data (Marenco et al. 2012) suggest that the strata of the Virgin Formation did not accumulate under oxygen-restricted conditions. This view is well supported by the faunal analysis of Hofmann et al. (2013b). The base of the Spathian, which has been sampled in the Thaynes Group only (this study), is taxonomically and ecologically less diverse than the benthic communities of the Virgin Formation. This difference may be partly due to more advanced recovery in the slightly younger Virgin Formation, but it appears also possible that the main cause is an onshore-offshore trend with higher diversities occurring more proximally (i.e. in the Virgin Formation), as already observed in the Griesbachian–Dienerian and Smithian. In addition, there are fewer samples from the Spathian Thaynes Group than from the Virgin Formation, which possibly adds a bias when data are directly compared. A preliminary comparison with data from the western tropical Tethys (Hofmann et al. 2013b, and references therein) suggests a significant interregional early Spathian recovery pulse.

Patterns in alpha- and beta-diversity. Eurytopicity has frequently been cited as a typical trait of Early Triassic faunas (e.g. Schubert and Bottjer 1995) and was usually interpreted as evidence for ongoing environmental stress (e.g. Pruss and Bottjer 2004; Boyer et al. 2004; Mata and Bottjer 2011). An alternative explanation has been proposed by Hofmann et al. (2013a, b), who suggested that reduced competition after the end-Permian mass extinction allowed species to exploit virtually the full range of their fundamental niches until competition exceeded a certain threshold. Accordingly, the prediction was made that an increase of within-habitat diversity (alpha diversity) precedes

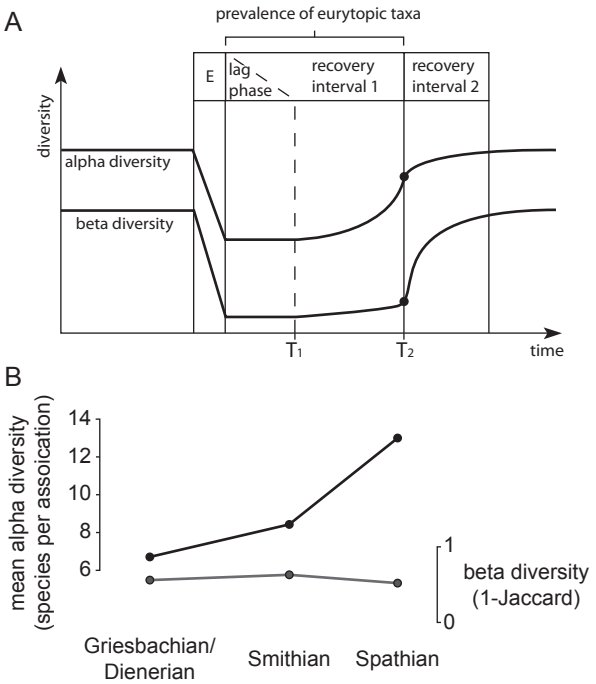

FIG. 22. Generalized model (after Hofmann et al. 2013b) illustrating the role of habitat saturation in recovery processes. The drop of alpha-diversity in course of an extinction (E) leads to a corresponding loss of beta-diversity and a highly reduced competition among species. A lag phase marks a time interval in which no significant radiation and increase in alpha-diversity is observed (Erwin 2001). After initial diversification (T1, start of recovery interval 1), competition within habitats increases following recovering alpha-diversity. Beta-diversity remains low throughout this interval because adding new species does not result in significant competition for resources. Eventually, alpha-diversity reaches a threshold value where a critical number of species competes for same, limited resources. The time when this habitat saturation is reached is herein referred to as T2. From this time onward (recovery interval 2), species are increasingly restricted to particular niches because of competitive exclusion from neighbouring habitats. Recovery interval 2 ends when all curves level off. Logistic growth of alpha-diversity is adopted from Erwin (2001). B, Test of the model based with own field data. Data for the Griesbachian/Dienerian from the Dinwoody Formation (Hofmann et al. 2013a). Data for the Smithian from the Sinbad Formation and the Smithian part of the Thaynes Group (this study). Data for the Spathian from the Virgin Formation (Hofmann et al. 2013b).

an increase of between-habitat diversity (beta diversity) during rediversifications from mass extinction events (Fig. 22A). This explanation accounts for the conflicting observations of (i) a relatively advanced ecological recovery and high within-habitat (alpha) diversity contrasted by (ii) the eurytopic character of most species, expressed in ongoing low beta diversity.

Our data from the Lower Triassic of the western US allow testing the prediction of the model for the first recovery phase, which is documented in three consecutive time-slices: the Griesbachian–?lower Dienerian of the Dinwoody Formation (Hofmann et al. 2013a), the Smithian Thaynes Group (this paper), and the Spathian part of the Thaynes Group (this paper) together with the late early Spathian Virgin Formation (Hofmann et al. 2013b). The data confirm the model prediction that alpha-diversity increases during the first phase whereas beta diversity remains stable (Fig. 22B). The somewhat lower beta diversity of the Virgin Limestone is most likely due to the much shorter time interval and smaller outcrop area of the Spathian samples. Further work is necessary to confirm (i) whether the post Early Triassic diversification of marine invertebrates is associated with an increase in beta diversity whereas average alpha-diversity remained stable and (ii) whether the post-recovery level of beta-diversity is comparable to pre-extinction times.

CONCLUSIONS

In addition to the description of the benthic palaeoecology of the Thaynes Group and the Sinbad Formation of the western US, we presented a revised interpretation of the recovery from the end-Permian mass extinction at the tropical Eastern Panthalassa margin. The succession of faunas and palaeoecological parameters suggests that benthic ecosystems probably suffered from environmental perturbations during parts of the Dienerian but not from long-lasting deleterious conditions during the entire Early Triassic. The late Smithian-Spathian transition might have been another time of environmental stress, which however had no long-term effect on benthic ecosystems. Notable restoration signals are recorded in shallow shelf settings during the late Griesbachian to early Dienerian, the Smithian, and the early Spathian. Diversity of outer shelf communities remains rather low throughout the studied time interval. We interpret this to represent a general proximal-distal trend that reflects an evolutionary delay of rediversification in distal settings compared to more proximal settings where evolutionary innovations are concentrated (cf. Jablonski et al. 1983; Miller 1988). The wide environmental range of taxa probably relates to a non-actualistic low degree of competition in Early Triassic ecosystems. We conclude that the Early Triassic recovery pattern of benthic ecosystems was largely driven by intrinsic dynamics of low-competition ecosystems and short-lived environmental perturbations.

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REFERENCES

ABERHAN, M. 1992. Palökologie und zeitliche Verbreitung benthischer Faunengemeinschaften im Unterjura von Chile. Beringeria, 5, 1–174.

— 1994. Guild-structure and evolution of Mesozoic benthic shelf communities. PALAIOS, 9, 516–545.

ADAMS, H. and ADAMS, A. 1858. The genera of recent Mollusca arranged according to their organization, 2. Bivalvia. John van Voorst, London, 661 pp.

ALLASINAZ, A. 1972. Revisione dei Pettinidi Triassici. Rivista Italiana di Paleontologia e Stratigrafia, 78, 189–428.

AMALIZKY, W. 1892. Ueber die Anthracosien der Permformation Russlands. Palaeontographica, 39, 125–213.

BAMBACH, R. K. 1977. Species richness in marine benthic habitats through the Phanerozoic. Paleobiology, 3, 152–167.

BANDEL, K. 1993. Caenogastropoda during Mesozoic times. Scripta Geologica, Special issue, 2, 7–56.

— 2007. Description and classification of Late Triassic Neritomorpha (Gastropoda, Mollusca) from the St Cassian Formation, Italien Alps. Bulletin of Geosciences, 82, 215–274.

BATTEN, R. L. and STOKES W.L. 1986. Early Triassic gastropods from the Sinbad Member of the Moenkopi Formation, San Rafael Swell, Utah. American Museum Novitates, 2864,1–33.

BEGG, J. G. and CAMPBELL, H. J. 1985. Etalia, a new Middle Triassic (Anisian) bivalve from New Zealand, and its relationship with other pteriomorphs. New Zealand Journal of Geology and Geophysics, 28, 725–741.

BEURLEN, K. 1944. Beiträge zur Stammesgeschichte der Muscheln. Sitzungsberichte der mathematisch-naturwissenschaftlichen Abteilung der Bayerischen Akademie der Wissenschaften zu München, 1, 133–145.

— 1954. As faunas de lamellibranquios do sistema genduanico no Parana. p. 107–136, pls 1–7. In LANGE, F. W. (ed.) Paleontologia do Parana. Comissao de Comemoracoes do Centenario do Parana, Curitiba.

BIERNAT, G. and EMIG, C.C. 1993: Anatomical distinctions of the Mesozoic brachiopods. Acta Palaeontologica Polonica, 38, 1–20.

BITTNER, A. 1891. Triaspetrefakten von Balia in Kleinasien. Jahrbuch der kaiserlich-königlichen Geologischen Reichsanstalt, 41, 97–116.

— 1898. Beiträge zur Paläontologie, insbesondere der triadischen Ablagerungen centralasiatischer Hochgebirge. Jahrbuch der k. k. geologischen Reichsanstalt, 48, 689–718.

— 1899. Trias–Ablagerungen des Süd–Ussuri–Gebietes in der ostsibirischen Küstenprovinz. Mémoires du Comité Géologique, 7, 1–35.

— 1901a. Ueber Pseudomonotis Telleri und verwandte Arten der unteren Trias. Jahrbuch der k.k. Geologischen Reichsanstalt, 50, 559–592.

— 1901b. Lamellibranchiaten aus der Trias des Bakonyer Waldes, Abhandlung 3. 1–107, pls 1–9. In HÖLZEL, E. (ed.). Resultate der wissenschaftlichen Erforschung des Balatonsees, Band 1, Teil 1, Anhang: Palaeontologie der Umgebung des Balatonsees, Band 2. Balaton-Ausschuss der Ungarischen Geographischen Gesellschaft, Wien.

BLAKEY, R 1974. Bulletin (Utah Geological and Mineral Survey). Stratigraphic and depositional analysis of the Moenkopi Formation, southeastern Utah. Utah Geological and Mineral Survey, [Salt Lake City], iv, 81 p.

— 2012. Global Paleogeography. http://www2.nau.edu/rcb7/globaltext2.html (accessed May 2012).

BOTTJER, D. J., SCHUBERT, J. K. and DROSER, M. L. 1996. Comparative evolutionary palaeoecology: assessing the changing ecology of the past. Geological Society, London, Special Publications, 102,1–13.

BOYER, D. L., BOTTJER, D. J. and DROSER, M. L. 2004. Ecological signature of Lower Triassic shell beds of the western United States. Palaios, 19, 372–380.

BRAYARD, A., NÜTZEL, A., STEPHEN, D. A., BYLUND, K. G., JENKS, J. and BUCHER, H. 2010. Gastropod evidence against the early Triassic Lilliput effect. Geology, 38, 147–150.

— ESCARGUEL, G., BUCHER, H., MONNET, C., BRÜHWILER, T., GOUDEMAND, N., GALFETTI, T. and GUEX, J. 2009. Good genes and good luck: Ammonoid diversity and the end-permian mass extinction. Science, 325, 1118–1121.

— BYLUND, K.G., JENKS, J.F., STEPHEN, D.A., OLIVIER, N., ESCARGUEL, G., FARA, E. and VENNIN, E., 2013a. Smithian ammonoid faunas from Utah: implications for Early Triassic biostratigraphy, correlation and basinal paleogeography. Swiss Journal of Paleontology.

— VENNIN, E., OLIVIER, N., BYLUND, K. G., JENKS, J., STEPHEN, D. A., BUCHER, H., HOFMANN, R., GOUDEMAND, N. and ESCARGUEL, G. 2011. Transient metazoan reefs in the aftermath of the end-Permian mass extinction. Nature Geoscience, 4, 693–697.

BROGLIO LORIGA, C. and MIRABELLA, S. 1986. Il genere Eumorphotis Bittner 1901 nella biostratigrafia dello Scitico, Formazione di Werfen (Dolomiti). Memorie di Scienze Geologiche, 38, 245–274.

BRONN, H. G. 1849. Index Palaeontologicus oder Übersicht der bis jetzt bekannten fossilen Organismen. Zweite Abtheilung. Enumerator palaeontologicus: Systematische Zusammenstellung und geologische Entwickelungs–Gesetze der organischen Reiche. Schweizerbart, Stuttgart, 776 pp.

CARR, T.R. and PAULL, R.K. 1983, Early Triassic Stratigraphy and Paleogeography of the Cordilleran Miogeocline, In REYNOLDS, A. and DOLLY, E.D. (eds). Mesozoic Paleogeography of the West-Central United States, Denver, SEPM, 39–55.

CARTER, J. G. and HAUTMANN, M. 2011. Shell Microstructure of the Basal Pectinid Pleuronectites Laevigatus: Implications for Pectinoid Phylogeny (Mollusca: Bivalvia: Pteriomorphia). Journal of Paleontology, 85, 464–467.

CATULLO, T. A. 1846. Memoria geognostico–paleozoica sulle Alpi Venete. Memorie della Società Italiana delle scienze residente in Modena, 24, 1–158.

CAVAROC, V. V. and FLORES R.M. 1991. Red beds of the Triassic Chugwater Group,
Southwestern Powder River Basin, Wyoming. U.S. Geological Survey Bulletin 1917-E, 17 p.

CHAVAN, A. 1954. Les Pleurophorus et genres voisins. Cahiers Géologiques Seyssel, 22, 200.

CIRIACKS, K. W. 1963. Permian and Eotriassic bivalves of the Middle Rockies. Bulletin of the American Museum of Natural History, 125, 1–100.

CLARK, D. L. and CARR, T. R. 1984. Conodont biofacies and biostratigraphic schemes in western North America: A model. Geological Society of America Special Paper, 196, 1–9.

COLLINSON, J. W. and HASENMUELLER, W. A. 1978. Early Triassic paleogeography and biostratigraphy of the Cordilleran miogeosyncline, In HOWELL, D. G., and Mcdougall, K. A. (eds.), Mesozoic paleogeography of the western United States. Society of Economic Paleontologists and Mineralogists, Pacific Section, Pacific Coast Paleogeography Symposium, 2,175–87.

COSSMANN, M. 1895. Essais de Paléoconchologie Comparée. Première Livraison. M. Cossmann, Comptoir Géologique, Paris, 161 pp

— 1902. Rectification de nomenclature. Revue critique de la nomenclature, 6, pp. 233.

— 1915. Étude complementaire sur le Charmoutien de la Vendée. Mémoires de la Société linnéenne de Normandie, Section geologique, 33, 113–159.

COX, L. R. 1929. A synopsis of the Lamellibranchia and Gastropoda of the Portland beds of England. Part 1. Lamellibranchiata. Proceedings of the Dorset Natural History and Archaeological Society, 50, 131–202.

— 1962. Newgenera and subgenera of Mesozoic Bivalvia. Palaeontology, 4, 592–598.

— 1964. Notes concerning the taxonomy and nomenclature of fossil Bivalves (mainly Mesozoic). Proceedings of the Malacological Society of London, 36, 39–48.

— NEWELL, N. D., BOYD, D. W., BRANSON, C. C., CASEY, R., CHAVAN, A., COOGAN, A. H., DECHASEUX, C., FLEMING, C. A., HAAS, F., HERTLEIN, L . G., KAUFFMAN, E.G., MYRA KEEN, A., LA ROCQUE, A., MC ALASTER, A. L., MOORE, R. C., NUTTALL, C. P., PERKINS, B. F., PURI, H. S., SMITH, L. A., SOOT-RYEN, T. STENZEL, H. B. TRUEMAN, E. R., TURNER, R. D. AND J. WEIR. 1969. Bivalvia. In: Moore, R. C. (ed.), Treatise on invertebrate paleontology. Part N. Mollusca 6, 1224 S., Boulder, Colorado and Lawrence, Kansas (Geological Society of America and University of Kansas Press).

CUVIER, G. 1797–1798. Tableau élémentaire de l'histoire naturelle des animaux. Paris Baudouin, 710 p.

DALL, W. H. 1899. Pelecypoda, 346–429, In ZITTEL, K. A. and EASTMAN C. R. VON (eds) Text-book of Palaeontology. Macmillan & Co., New York.

DICKINS, J. M. 1957. Lower Permian pelecypods and gastropods from the Carnarvon Basin, Western Australia. Commonwealth of Australia, Department of National Development, Bureau of Mineral Resources, Geology and Geophysics, Bulletin, 41, 1–71.

DIENER, C. 1923. Lamellibranchiata triadica. Fossilium catalogus I: Animalia. Pars 19. W. Junk, Berlin, 257 pp.

DUMERIL, A. M. C. 1806. Zoologie analytique ou méthode naturelle de classification des animaux. Allais, Paris, xxiv, 364 p.

ERWIN, D. H. 2001. Lessons from the past: Biotic recoveries from mass extinctions. Proceedings of the National Academy of Sciences of the United States of America, 98, 5399–5403.

FANG, Z-J., J. CHEN, C. CHEN, J. SHA, X. LAN, AND WEN. S. 2009. Supraspecific taxa of the Bivalvia first named, described, and published in China (1927–2007). The University of Kansas Paleontological Contributions, New Series, 17, 1–157.

FÉRUSSAC, A. E. DE. 1822. Tableaux systématiques des animaux mollusques classés en familles naturelles, dans lesquels on a établi la concordance de tous les systèmes; suivis d'un prodrome général pour tous les mollusques terrestres ou fluviatiles, vivants ou fossiles. Bertrand, Paris, 111 pp.

FLEMING, J. 1828. A history of British animals, exhibiting the descriptive characters and systematical arrangement of the genera and species of quadrupeds, birds, reptiles, fishes, Mollusca and Radiata of the United Kingdom; including the indigenous, extirpated, and extinct kinds; together with periodical and occasional visitants. Bell and Bradfute, Edinburgh, xxiii + 554 pp.

FRECH, F. 1907. Die Leitfossilien der Wefener Schichten und Nachträge zur Fauna des Muschelkalkes der Cassianer und Raibler Schichten sowie des Rhaet und des Dachsteinhauptdolomites (Hauptdolomit). Resultate der wissenschaftlichen Erforschung des Balatonsees, Anhang: Palaeontologie der Umgebung des Balatonsees, 1, 1–95.

FÜRSICH, F. T. 1984. Paleoecology of Boreal Invertebrate Faunas from the Upper Jurassic of Central East Greenland. Palaeogeography Palaeoclimatology Palaeoecology, 48, 309–364.

— and WENDT, J. 1977. Biostratinomy and palaeoecology of the cassian formation (Triassic) of the Southern Alps. Palaeogeography, Palaeoclimatology, Palaeoecology, 22, 257–323.

GEINITZ, H. B. 1842. Über einige Petrefakten des Zechsteins und Muschelkalks. Neues Jahrbuch für Mineralogie, 1842, 576–579.

GEYER, G, HAUTMANN, MT, HAGDORN, H, OCKERT, W AND STRENG, M. 2005. Well-preserved molluscs from the Lower Keuper (Ladinian) of Hohenlohe (Southwest Germany). Palaeontologische Zeitschrift, 79, 429–460.

GIEBEL, C. 1855. Kritisches über die Myophorien des Muschelkalkes. Zeitschrift für die gesamten Naturwissenschaften, 5, 34–36.

GIRTY, G. H. 1927. Descriptions of new species of Carboniferous and Triassic fossils. In Mansfield, G. R. Geography geology and mineral resources of part of southeastern Idaho With descriptions of Carboniferous and Triassic fossils. US Geological Survey Professional Paper, 152, 453 p.

GOLDFUS S, A. 1833–1840. Petrefacta Germaniae. Abbildungen und Beschreibungen der Petrefacten Deutschlands und der angränzenden Länder, unter Mitwirkung des Herrn Grafen Georg zu Münster, herausgegeben von August Goldfuss. Zweiter Teil. Arnz and Co., Düsseldorf, 211 pp., 84 pls.

GOODSPEED, T.H. and LUCAS, S.G. 2007. Stratigraphy, sedimentology, and sequence stratigraphy of the Lower Triassic Sinbad Formation, San Rafael Swell, Utah. New Mexico Mu-

seum of Natural History and Science Bulletin, 40, 91–102.

GORYANSKY, V. YU . and POPOV, L. E. 1985. Morphology, systematic position and origin of the inarticulate brachiopods with calcareous shells. Paleontologicheskii Zhurnal, 1985, 3–14.

GRASBY, S. E., BEAUCHAMP, B., EMBRY, A. and SANEI, H. 2013. Recurrent Early Triassic ocean anoxia. Geology, 41, 175–178.

GRAY, J. E. 1847. A list of the genera of Recent Mollusca, their synonyms and types. Proceedings of the Zoological Society of London, 15, 129–219.

GROBBEN, C. 1894. Zur Kenntnis der Morphologie, der Verwandtschaftsverhältnisse und des Systems der Mollusken. Sitzungsberichte der Akademie der Wissenschaften Wien, 103, 61–86.

GUEX, J., HUNGERBÜHLER, A., JENKS, J. F., O'DOGHERTY, L., ATUDOREI, V., TAYLOR, D. G., BUCHER, H. and BARTOLINI, A. 2010. Spathian (lower triassic ammonoids from western usa (idaho, california, utah and nevada. Mémoires de Géologie Lausanne, 49, 82.

HALLAM, A. 1991. Why was there a delayed radiation after the end-Palaeozoic
extinctions? Historical Biology, 5, 257–262.

HAMMER, Ø. and HARPER, D. A. T. 2006. Paleontological data analysis. Blackwell Pub., Malden, MA, x, 351 p.

— HARPER, D. A. T. and RYAN, P. D. 2001. Past: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica, 4,

HAUTMANN, M. 2004. Early Mesozoic evolution of alivincular bivalve ligaments and its implications for the timing of the "Mesozoic marine revolution". Lethaia, 37, 165–172.

HAUTMANN, M. 2008. Taxonomy and phylogeny of the Triassic bivalve families Mysidiellidae Cox, 1964 and Healeyidae new family. Journal of Paleontology, 82, 555–564.

— 2010. The first scallop. Paläontologische Zeitschrift, 84, 317–322.

— 2011. Suborder Entoliidina Hautmann, nov.; Family Pleuronectitidae Hautmann, nov.; Family Antijaniridae Hautmann, nov.; Family Ornithopectinidae Hautmann, nov. In CARTER et al., A Synoptical Classification of the Bivalvia (Mollusca). Paleontological Contributions, 4, 1–47.

— and HAGDORN, H. 2013. Oysters and oyster-like bivalves from the Middle Triassic Muschelkalk of the Germanic Basin. Palaeontologische Zeitschrift, 87, 19–32.

— and NÜTZEL, A. 2005. First record of a heterodont bivalve (Mollusca) from the Early Triassic : Palaeoecological significance and implications for the 'Lazarus problem'. Palaeontology, 48, 1131–1138.

— SMITH, A. B., McGOWAN, A. J. and BUCHER, H. 2013. Bivalves from the Olenekian (Early Triassic) of southwestern Utah: Systematics and evolutionary significance. Journal of Systematic Palaeontology, 11, 263–293.

— BUCHER, H., BRÜHWILER, T., GOUDEMAND, N., KAIM, A. and NÜTZEL, A. 2011. An unusually diverse mollusc fauna from the earliest Triassic of South China and its implications for benthic recovery after the end-Permian biotic crisis. Geobios, 44, 71–85.

HERMANN, E., HOCHULI, P. A., MÉHAY, S., BUCHER, H., BRÜHWILER, T., WARE, D., HAUTMANN, M., ROOHI, G., UR-REHMAN, K. and YASEEN, A. 2011. Organic matter and palaeoenvironmental signals during the Early Triassic biotic recovery: The Salt Range and Surghar Range records. Sedimentary Geology, 234, 19–41.

HERTWIG, C. W. T. R. 1895. Lehrbuch der Zoologie (third edition). Fischer, Jena, 599 p.

HOFMANN, R., HAUTMANN, M. and BUCHER, H. 2013a. A new paleoecological look at the Dinwoody Formation (Lower Triassic, western US): intrinsic versus extrinsic controls on ecosystem recovery after the end-Permian mass extinction. Journal of Paleontology, 87, 854–880.

— HAUTMANN, M., WASMER, M. and BUCHER, H. 2013b. Palaeoecology of the Spathian Virgin Formation (Utah, USA) and Its Implications for the Early Triassic Recovery. Acta Palaeontologica Polonica, 58, 149–173.

HOLMER, L. E. and BENGTSON, P. 2009. The first occurrence of a lingulid brachiopod from the Cretaceous of Sergipe, Brazil, with a restudy of 'Lingula' bagualensis Wilckens, 1905 from southern Patagonia. Paläontologische Zeitschrift, 83, 255–266.

— GOUDEMAND, N., WASMER, M., BUCHER, H. and HAUTMANN, M. 2011. New trace fossil evidence for an early recovery signal in the aftermath of the end-Permian mass extinction. Palaeogeography Palaeoclimatology Palaeoecology, 310, 216–226.

HOOVER, P. R. 1979. Early Triassic Terebratulid brachiopods from the western interior of the United States. United States Geological Survey Professional Paper, 1057, 1–21.

ICHIKAWA, K. 1958. Zur Taxionomie und Phylogenie der Triadischen "Pteriidae" (Lamellibranch.). Palaeontographica, Abt. A, 111, 131–212.

JABLONSKI, D., SEPKOSKI, J. J., BOTTJER, D. J. and SHEEHAN, P. M. 1983. Onshore-Offshore Patterns in the Evolution of Phanerozoic Shelf Communities. Science, 222, 1123–1125.

KAIM, A. 2009. Gastropods. In SHIGETA, Y., ZAKHAROV, YU. D., MAEDA, H. and POPOV, A. M. (eds). The Lower Triassic system in the Abrek Bay area, south Primorye, Russia. National Museum of Nature and Science Monographs, 38, 141–156.

— and NÜTZEL, A. 2011. Dead bellerophontids walking - The short Mesozoic history of the Bellerophontoidea (Gastropoda). Palaeogeography Palaeoclimatology Palaeoecology, 308, 190–199.

— NÜTZEL, A., HAUTMANN, M. and BUCHER, H. 2013a. Early Triassic gastropods from Salt Range, Pakistan. Bulletin of

Geosciences, 88, 505–516

— NÜTZEL, A., BUCHER, H., BRÜHWILER, T. and GOUDEMAND, N. 2010. Early Triassic (Late Griesbachian) gastropods from South China (Shanggan, Guangxi). Swiss Journal of Geosciences, 103, 121–128.

KASHIYAMA, Y. and OJI, T. 2004. Low-diversity shallow marine benthic fauna from the Smithian of northeast Japan: paleoecologic and paleobiogeographic implications. Paleontological Research, 8, 199-218.

KING, W. 1848. A Catalogue of the Organic Remains of the Permian Rocks of Northumberland and Durham. Published by the author, Newcastle-upon-Tyne, 16 pp.

— 1850. A monograph of the Permian Fossils of England. Palaeontographical Society, London, 258 pp.

KIPARISOVA, L. D. 1938. Nizhnetriasovye plastinchatozhabernye Ussurijskogo kraya. Trudy Geologicheskogo Instituta, 7, 197–311. [in Russian].

KITTL, E. 1904. Geologie der Umgebung von Sarajevo. Jahrbuch der Geologischen Reichsanstalt, 53 [for 1903], 707–738.

KNIGHT, J.B. 1931. The gastropods of the St. Louis, Missouri, Pennsylvanian outlier: the Subulitidae. Journal of Paleontology, 5, 177–229.

KOKEN, E. 1892. Ueber die Gastropoden der rothen Schlernschichten nebst Bemerkungen über Verbreitung und Herkunft einiger triassischer Gattungen. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, 2, 25–36.

— 1896 Die Leifossilien, ein Handbuch für den Unterricht und das Bestimmen von Versteinerungen. Leipzig, 848 pp.

KONINCK, L.G. DE 1881. Faune du calcaire carbonifère de la Belgique, 3e partie, Gastéropodes. Musée Royale d'Historie Naturelle Belgique Annales, Série Paléontologique, 6, 1–170.

— 1883. Faune du calcaire carbonifére de la Belgique, quartiéme partie. Gastéropodes. Musée Royal d'Histoire Naturelle de Belgique Annales, Série Paléntologique, 8, 1 – 240.

KOROBKOV, I. A. 1960. Anisomyaria. p. 83, In EBERZIN, A. G. (ed.) Osnovy Paleontologii, Volume 3. Academy Nauk USSR, Moscow.

KRYSTYN, L., RICHOZ, S., BAUD, A. and TWITCHETT, R. J. 2003. A unique Permian-Triassic boundary section from the Neotethyan Hawasina Basin, Central Oman Mountains. Palaeogeography Palaeoclimatology Palaeoecology, 191, 329–344.

KUMAGAE, T. and NAKAZAWA, K. 2009. Bivalves. In SHIGETA, Y., ZAKHAROV, YU. D., MAEDA, H. and POPOV, A. M. (eds). The Lower Triassic system in the Abrek Bay area, south Primorye, Russia. National Museum of Nature and Science Monographs, 38, 156–173.

KUMMEL, B. and STEELE, G. 1962. Ammonites from the Meekoceras-Gracilitatus Zone at Crittenden-Spring, Elko County, Nevada. Journal of Paleontology, 36, 638–703.

LEPSIUS, R. 1878. Das westliche S¨udtirol. Verlag Wilhelm Hertz, Berlin, 375 pp.

LINNAEUS, C. 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tomus I. Editio Decima. Laurentius Salvius, Stockholm, 824 pp.

LUCAS, S.G., KRAINER, K., and MILNER, A.R. 2007, The type section and age of the Timpoweap Member and stratigraphic nomenclature of the Triassic Moenkopi Group in Southwestern Utah. New Mexico Museum of Natural History and Science Bulletin, 40, 109–117.

MARENCO, P. J., GRIFFIN, J. M., FRAISER, M. L. and CLAPHAM, M. E. 2012. Paleoecology and geochemistry of Early Triassic (Spathian) microbial mounds and implications for anoxia following the end-Permian mass extinction. Geology, 40, 715–718.

MARWICK, J. 1953. Divisions and faunas of the Hokonui system (Triassic and Jurassic). New Zealand Geological Survey, Paleontological Bulletin, 21, 1–141.

MATA, S. A. and BOTTJER, D. J. 2011. Origin of Lower Triassic microbialites in mixed carbonate-siliciclastic successions: Ichnology, applied stratigraphy, and the end-Permian mass extinction. Palaeogeography, Palaeoclimatology, Palaeoecology, 300, 158–178.

MCGOWAN, A. J., SMITH, A. B. and TAYLOR, P. D. 2009. Faunal diversity, heterogeneity and body size in the Early Triassic: testing post-extinction paradigms in the Virgin Limestone of Utah, USA*. Australian Journal of Earth Sciences, 56, 859-872.Meek and Hayden, 1864

MEEK, F. B. 1877. Part I Palaeontology. In KING, C. (ed.) Annual Report to the Secretary of War on the U.S. geological exploration of the Fortieth Parallel 4. Government Printing Office, Washington. 1–197

— and HAYDEN, F. V. 1864. Palaeontology of the Upper Missouri. Smithsonian Contributions to Knowledge, 14, 1–135.

MENKE, C.T. 1828, Synopsis methodica molluscorum generum omnium et specierum earum quae in Museo Menkeano adservantur. Pyrmonti, 91 p.

MILLER, A. I. 1988. Spatio-temporal transitions in Paleozoic Bivalvia: An analysis of North American fossil assemblages. Historical Biology, 1, 251–273.

MILLER, S. A. 1877. The American Paleozoic fossils: a catalogue of the genera and species. Published by the author, Cincinnati, 334 p.

MORISITA, M. 1959. Measuring of interspecific association and similarity between communities. Mem. Fac. Sci. Kyushu Univ. Ser. E (Biol.), 3, 65–80.

MÜNSTER, G. GRAF ZU, 1841. Beiträge zur Petrefacten–Kunde. IV. Beschreibung und Abbildung der in den Kalkmergelschichten von St. Cassian gefundenen Versteinerungen. Buchner´sche Buchhandlung. 152 p.

NERI, C. and POSENATO, R. 1985. New biostratigraphical data on uppermost Werfen formation of western Dolomites

(Trento, Italy). Geologisch-Paläontologische Mitteilungen Innsbruck, 14, 83–107.

NEUMAYR, M. 1884. Zur Morphologie des Bivalvenschlosses. Sitzungsberichte der Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse, Abteilung. 1, 88, 385–418.

NEWELL, N. D. 1938. Late Paleozoic Pelecypods: Pectinacea. State Geological Survey of Kansas Publications, 10 [for 1937], 1–123.

— 1942. Late Paleozoic pelecypods: Mytilacea. University of Kansas Publications, State Geological Survey of Kansas, 10, 1–115.

— 1965. Classification of the Bivalvia. American Museum Novitates, 2206, 1–25.

— 1969. Order Modiomorphoida Newell, new order. P. N393 In R. C. MOORE, R. C. (ed). Treatise on Invertebrate Paleontology, Part N, Mollusca 6, Volume 1. Geological Society of America and University of Kansas Press, Boulder.

— and BOYD, D. W. 1995. Pectinoid bivalves of the Permian-Triassic crisis. Bulletin of the American Museum of Natural History, 227, 5–95.

— and KUMMEL, B. 1942. Lower Eo-Triassic stratigraphy, western Wyoming and southeast Idaho. Geological Society of America Bulletin, 53, 937–996.

NEYMAN, A. A. 1967. Limits to the application of the trophic group concept in benthic studies. Oceanology, 7, 149–155.

NÜTZEL, A. 2005. A new Early Triassic gastropod genus and the recovery of gastropods from the Permian/Triassic extinction. Acta Palaeontologica Polonica, 50, 19–24.

— and SCHULBERT, C. 2005. Facies of two important Early Triassic gastropod lagerstätten: implications for diversity patterns in the aftermath of the end-Permian mass extinction. Facies, 51, 480–500.

ORBIGNY, A. D'. 1850. Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnés faisant suite au coursélémentaire der paléontologie et géologie stratigraphiques. Deuxième Volume. Masson, Paris, 427 pp.

PAULL, R.A., and PAULL, R.K., 1993, Interpretation of Early Triassic nonmarine-marine relations, Utah, USA. New Mexico Museum of Natural History and Science Bulletin, 3, 403–409.

PENG, Y. Q. and SHI, G. R. 2008. New Early Triassic Lingulidae (Brachiopoda) genera and species from South China. Alcheringa, 32, 149–170.

PERRY, D. G. and CHATTERTON, B. D. E. 1979. Late Early Triassic brachiopod and conodont fauna, Thaynes Formation, Southeastern Idaho. Journal of Paleontology, 53, 307–319.

POBORSKI, S. J. 1954. Virgin formation (Triassic) of the St. George, Utah, area. Bulletin of the Geological Society of America, 65, 971–1006.

POSENATO, R. 2008. Anisian (Middle Triassic) bivalves from the Dolomites (Italy). Neues Jahrbuch Fur Geologie Und Palaontologie-Abhandlungen, 247, 93–115.

— PELIKAN, P. and HIPS, K. 2005. Bivalves and brachiopods near the Permian-Triassic boundary from the Bukk Mountains (Balvany-North section, Northern Hungary). Rivista Italiana di Paleontologia e Stratigrafia, 111, 215–232.

PRUSS, S. B. and BOTTJER, D. J. 2004. Early Triassic trace fossils of the western United States and their implications for prolonged environmental stress from the end-permian mass extinction. PALAIOS, 19, 551–564.

RAFINESQUE, C. S. 1815. Analyse de la nature ou tableau de l'a Univers et des corps organisés. Jean Barravecchia, Palermo, 224 pp.

RICHTHOFEN , F. VON. 1860. Geognostische Beschreibung der Umgebung von Predazzo, Sanct Cassian und der Seiser Alpe in Süd-Tyrol. Gotha (Perthes), 327 pp.

RODLAND, D. L. and BOTTJER, D. J. 2001. Biotic recovery from the end-permian mass extinction: Behavior of the inarticulate brachiopod Lingula as a disaster taxon. PALAIOS, 16, 95–101.

ROMANO, C., GOUDEMAND, N., VENNEMANN, T. W., WARE, D., SCHNEEBELI-HERMANN, E., HOCHULI, P. A., BRUHWILER, T., BRINKMANN, W. and BUCHER, H. 2013. Climatic and biotic upheavals following the end-Permian mass extinction. Nature Geoscience, 6, 57–60.

SALVINI-PLAWEN, L.V. 1980. A reconsideration of systematics in the Mollusca (phylogeny and higher classification). Malacologica, 19, 249–278.

SCHAUROTH, K. VON. 1859. Kritisches Verzeichnis der Versteinerungen der Trias im Vicentinischen. Sitzungsberichte der Kaiserlichen Akademie derWissenschaften Wien, Mathematisch-Naturwissenschaftliche Classe, 34,283–356.

SCHUBERT, J. K. and BOTTJER, D. J. 1995. Aftermath of the Permian-Triassic mass extinction event: Paleoecology of Lower Triassic carbonates in the western USA. Palaeogeography, Palaeoclimatology, Palaeoecology, 116, 1–39.

SCHWARDT, A. 1992. Revision der Wortheniella Gruppe (Archaeogastropoda) der Cassianer Schichten (Trias, Dolomiten). Annalen des Naturhistorischen Museums in Wien, 94. 23–57.

SEPKOSKI, J. J. 1988. Alpha, Beta, or Gamma - Where Does All the Diversity Go. Paleobiology, 14, 221–234.

SHA, J. 1995. Bivalves, In SHA, J. (ed) Palaeontology of Hoh Xil region, Qinghai Beijing, China, Science Press, (in Chinese with English abstract), 82–116,151–153.

— GRANT-MACKIE, J. A. 1996. Late Permian to Miocene bivalve assemblages from Hohxil, Qinghai-Xizang Plateau, China. Journal of the Royal Society of New Zealand, 26, 429–455.

SHIGETA, Y., ZAKAHAROV, Y. D., MAEDA, H., and POPOV, A. M. (eds.) 2009. The Lower Triassic System in the Abrek Bay area, South Primorye, Russia. National Museum of Nature and Science Monographs 38, Tokyo.

STANLEY, M. S. 1972. Functional Morphology and Evolution of Byssally Attached Bivalve Mollusks. Journal of Paleontology, 46,165–212.

STEHLI, F. G. 1965, Paleozoic Terebratulida. In R. C. MOORE, (ed), Treatise on Invertebrate Paleontology, Part H, Brachiopoda, v. 2: New York and Lawrence, Kans., Geol. Soc. America and Univ. Kansas Press, p. H730–H762.

STEPHEN, D.A., BYLUND, K., BYBEE, P.J., and REAM, W.J., 2010, Ammonoid beds in the Lower Triassic Thaynes Formation of western Utah, USA., In TANABE, K., SHIGETA, Y., SASAKI, T., and HIRANO, H., (eds), Cephalopods - Present and Past, Tokyo, Tokai University Press, 243–252.

STOLICZKA, F. 1870–1871. Cretaceous fauna of southern India. 3. The Pelecypoda, with a review of all known genera of this class, fossil and Recent. Geological Survey of India, Paleontologica Indica Memoirs, 6, 1–537.

THOMSON, J. A. 1926. A revision of the subfamilies of the Terebratulidae (Brachiopoda). Annals and Magazine of Natural History; Zoology, Botany and Geology, Series 9, 18 , 523–530.

TWITCHETT, R. J. and WIGNALL, P. B. 1996. Trace fossils and the aftermath of the Permo-Triassic mass extinction: Evidence from northern Italy. Palaeogeography, Palaeoclimatology, Palaeoecology, 124, 137–151.

VOKES, H. E. 1967. Genera of the Bivalvia: a systematic and bibliographic catalogue. Bulletins of American Paleontology, 51, 105–394.

WAAGEN, W. 1883. Productus Limestone Fossils, Part IV, fas. 2. Salt Range Fossils, Palaeontologia Indica, Series 13, 391–546.

— 1895. Salt–Range fossils, Vol. 2: Fossils from the Ceratite Formation. Pisces–Ammonoidea (Cephalopoda). Memoirs of the Geological Survey of India, Palaeontologia Indica, 13, 1–323.

WALLER, T. R. 1978. Morphology, morphoclines and a new classification of the Pteriomorphia (Mollusca: Bivalvia). Philosophical Transactions of the Royal Society of London, Ser. B, 284, 345–365.

— 2005. Systematic Palaeontology. 7–50. In WALLER, T. R. and STANLEY, G. D. 2005. Middle triassic pteriomorphian bivalvia (Mollusca) from the New Pass Range, west-central Nevada: Systematics, biostratigraphy, paleoecology, and paleobiogeography. Journal of Paleontology, 79, 1–58.

— 2006. Phylogeny of families in the Pectinoidea (Mollusca : Bivalvia): importance of the fossil record. Zoological Journal of the Linnean Society, 148, 313–342.

— and STANLEY, G. D. 2005. Middle triassic pteriomorphian bivalvia (Mollusca) from the New Pass Range, west-central Nevada: Systematics, biostratigraphy, paleoecology, and paleobiogeography. Journal of Paleontology, 79, 1–58.

WARE, D., JENKS, J. F., HAUTMANN, M. and BUCHER, H. 2011. Dienerian (Early Triassic) ammonoids from the Candelaria Hills (Nevada, USA) and their significance for palaeobiogeography and palaeoceanography. Swiss Journal of Geosciences,
104, 161–181.

WASMER, M., and HAUTMANN, M. 2012. Systematic Palaeontology. 1047–1065. In WASMER, M., HAUTMANN, M., HERMANN, E., WARE, D., ROOHI, G., UR-REHMAN, K., YASEEN, A. and BUCHER, H. 2012. Olenekian (Early Triassic) bivalves from the Salt Range and Surghar Range, Pakistan. Palaeontology, 55, 1043–1073.

— HAUTMANN, M., HERMANN, E., WARE, D., ROOHI, G., UR-REHMAN, K., YASEEN, A. and BUCHER, H. 2012. Olenekian (Early Triassic) bivalves from the Salt Range and Surghar Range, Pakistan. Palaeontology, 55, 1043–1073.

WENZ, W. 1938 Gastropoda, Teil I. In SCHINDEWOLF , O. H. (ed). Handbuch der Paläozoologie, Band. 6, Berlin, Borntraeger, pp. 1639.

WHEELEY, J. R. and TWITCHETT, R. J. 2005. Palaeoecological significance of a new Griesbachian (Early Triassic) gastropod assemblage from Oman. Lethaia, 38, 37–45.

WHITTAKER, R. H. 1972. Evolution and measurement of species diversity. Taxon, 21, 213-251.

WIGNALL, P. B. and HALLAM, A. 1992. Anoxia as a Cause of the Permian Triassic Mass Extinction - Facies Evidence from Northern Italy and the Western United-States. Palaeogeography Palaeoclimatology Palaeoecology, 93, 21–46.

WILCKENS, R. 1909. Paläontologische Untersuchung triadischer Faunen aus der Umgebung von Predazzo in Südtirol. Verhandlungen d. Naturhist.-Med. Vereins zu Heidelberg, pp. 151.

WILLIAMS, A., CARLSON, S. J., BRUNTON, C. H. C., HOLMER, L. E. and POPOV, L. 1996. A supra-ordinal classification of the Brachiopoda. Philosophical Transactions of the Royal Society B-Biological Sciences, 351, 1171–1193.

WINCHELL, A. 1865. Descriptions of newspecies of fossils from the Marshall Group, and its supposed equivalent in other states. Proceedings of the Academy of Natural Sciences of Philadelphia, 1865, 109–133.

WITTENBURG, P. von, 1908, Beiträge zur Kenntnis der Werfener Schichten Südtirols. Geologische und Palaeontologische Abhandlungen, 5, 251–289.

YIN, H. and YIN, J. 1983. Bivalves. In YANG, Z., YIN, H., XU, G., Wu, S., He, Y., LIU, G. and YIN, J. (eds). Triassic of the South Qilian Mountains. Geological Publishing House. Beijing, [In Chinese], 128–175.

YÜ, W. 1975. The Gastropod Fossils from the Qomolangma Feng Region. [in Chinese] 214 pp. Science Press, Peking.

ZIETHEN, C. H. Von 1830. Die Versteinerungen Württembergs. Verlag & Lithographie des Werkes Unsere Zeit, Stuttgart, 102 p.

ZITTEL , K.A. VON 1895. Grundzüge der Paläontologie (Palä0-zoologie), Abteilung I, Invertebrata, Oldenburg, München & Leipzig 971 p.

Chapter 5

Recovery dynamics of benthic marine communities from the Lower Triassic Werfen Formation (northern Italy)

"Die Unlust weiter zuleben
reicht zum Sterbenwollen nicht aus. "

Heinz Strunk, Fleckenteufel (2009, Rowohlt)

Recovery dynamics of benthic marine communities from the Lower Triassic Werfen Formation (northern Italy)

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Abstract: The Lower Triassic Werfen Formation of northern Italy represents an important archive for Early Triassic ecosystems. Based on quantitative community analysis using species level identifications, we reconstruct the recovery of benthic ecosystems after the end-Permian mass extinction throughout this unit. The analysis of benthic macrofossil communities shows that incipient recovery has taken place during the Griesbachian and the Griesbachian-Dienerian transition. A significant decline in environmental conditions is observed towards the end of the Dienerian. The Smithian part of the Werfen Formation is characterised by high siliciclastic imput, which cease during the Smithian-Spathian boundary interval. The Spathian marks the definite onset of recovery. The comparison of this pattern with other palaoegeographic regions suggests that both the Griesbachian recovery and the Dienerian decline were of interregional if not global extent, whereas the Smithian diversity low in the Werfen Formation is a local signal. In contrast to the recovery dynamics of ammonoids, the Smithian-Spathian boundary interval was no caesura for benthic ecosystems. The Spathian recovery pulse is possibly also an interregional event, at least in the palaeotropics. These results are at variance with the previously proposed scenario of persistent hostile conditions during the Griesbachian time interval. Instead, the apparently sluggish recovery of benthic ecosystems results from set-backs due to short-term environmental changes.

Key words: recovery • benthic ecosystems • Werfen Formation • palaeoecology • Early Triassic

THE restructuring of ecosystems in the aftermath of the end-Permian mass extinction has been a main research focus for more than two decades (e.g. Hallam 1991). However, several aspects of the biotic recovery are still poorly understood mainly owing to the limited taxonomic, stratigraphic and environmental resolution of available palaeontological data. A number of recent studies (Hautmann *et al.* 2011, 2013; Hofmann *et al.* 2013a, b, c) have shown that quantitative species level data allow for a much more differentiated analysis. A considerable advance in the understanding of the recovery was provided by the finding that ecosystems show unexpectedly high diversities soon after the extinction (Krystyn *et al.* 2003; Hautmann *et al.* 2011) and that the rather sluggish recovery possibly reflects short environmental perturbations later in the Early Triassic (Hofmann *et al.* 2011, 2013c) instead of persistent deleterious conditions that were previously assumed (Wignall and Hallam 1992; Twitchett and Wignall 1996). However, additional palaeoecological studies of continuous Lower Triassic successions are needed to fully understand the factors that controlled recovery from the greatest diversity collapse in metazoan history. The Werfen Formation of the Dolomites (Italy) has a rich historic record of palaeontological research and was also early recognised as a key locality for post-extinction studies (Wignall and Hallam, 1992; Twitchett and Wignall 1996). Quite surprisingly, a comprehensive analysis of its abundant benthic macrofauna has not been attempted yet. To close this gap, we present species-abundance data collected from the whole Werfen Formation, which allows us to track changes in the ecological and taxonomic composition of the benthic faunas and throughout the Early Triassic of the western tropical Tethys.

Localities, material, and methods

Fieldwork was carried out by RH and MH in May and August 2009 as well as in July and September 2011.

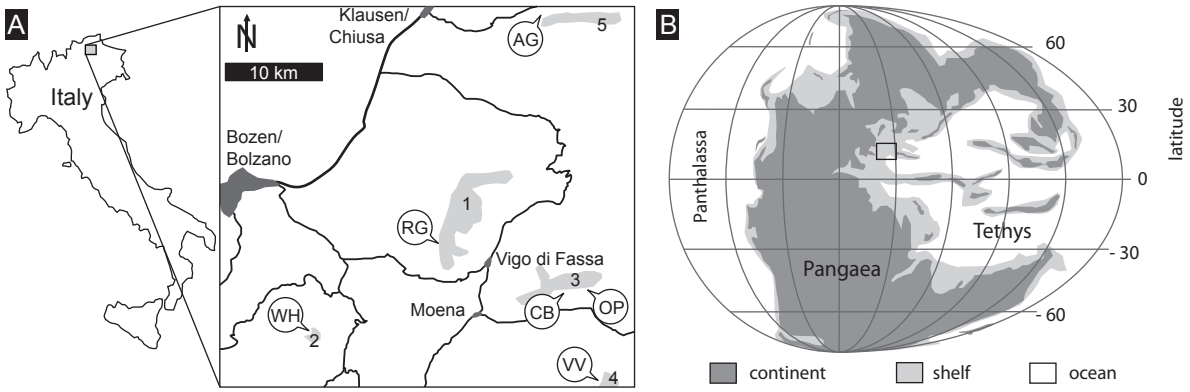

Fig. 1. A, Studied sections of the Dolomites. RG - Rosengarten, AG - Aferer Geisler, WH - Weißhorn, CB - Costabella, OP - L'Om Picol, VV - Val Venegia.Towns in dark grey. Mountain ranges in light grey: 1 - Rosengarten group (Catinaccio), 2 - Weißhorn (Corno Bianco), 3 Costabella Group, 4 - Pale di San Martino, 5 - Peitlerkofel group. B, Palaeogeographic position of the dolomite region during the Early Triassic. Palaeogeographic restoration after Blakey (2012).

Logged sections (Fig. 1A) include exposures in the western Dolomites in the Province of South Tyrol (Alto Adige) and Trentino. Bed-by-bed logging and fossil sampling was conducted at six sections cumulatively covering the whole Werfen Formation. We also logged and sampled each stratigraphic interval at least at two different localities. The majority of fossils were collected from limestone and to a lesser extent from (calcareous) sandstone and marls. Quantitative samples were obtained by mechanically decomposing large blocks from sample layers in order to extract identifiable fossil material. When necessary, standard invertebrate sample preparation techniques were later performed in the lab to work out morphologic details facilitating species-level identification. The comprehensive sedimentological analysis of Broglio Loriga *et al*. (1983) was used as a framework for interpretation of the depositional environment, added by own assessment of sedimentary facies in the field. Beds showing evidence of strong reworking, as for instance size-sorting, pronounced gradation or abundant abrasion of fossils, were not included in the quantitative analysis. Sampled intervals were found to represent autochthonous and para-autochthonous communities as bivalves were frequently observed in life position or are generally recorded as complete unabraded valves or molds of complete specimens. Fossils recognised herein include bivalves, gastropods, brachiopods and echinoderms. All identifiable fossils were counted on species level. The full faunal abundance list and a table of all benthic associations is given in Appendix (IV-E; V-D). For the cluster analysis, we used separate subsets for the (i) Mazzin Member, (ii) Seis/Siusi Member, (iii) Campil Member, and (iv) the Val Badia- and the Cencenighe Member in order to identify ecologic changes through time. The cluster analysis was carried with the software package PAST version 2.17c (Hammer *et al.* 2001) using unweighted paired group Q-mode cluster analysis and the Morisita (Morisita 1959) index of similarity, which was previously applied successfully in series of papers on benthic recovery in the Early Triassic of the western US (Hofmann *et al*. 2013b). All subclusters and respective samples with a Morisita-similarity of at least higher than 0.6 were pooled into associations (cf. Aberhan 1992). The species-abundance data of these associations were then used to obtain ranked species abundance, trophic nuclei, ecological pie-charts and rarefaction analysis. The trophic nucleus constitutes all species that contribute to at least 80 percent of total specimen number per association (Neyman 1967). An inverse measure of taxonomic evenness in samples is given as dominance index D as obtained from PAST (Hammer *et al*. 2001). Taxonomic diversity of samples (species richness) and alpha-diversity (species richness

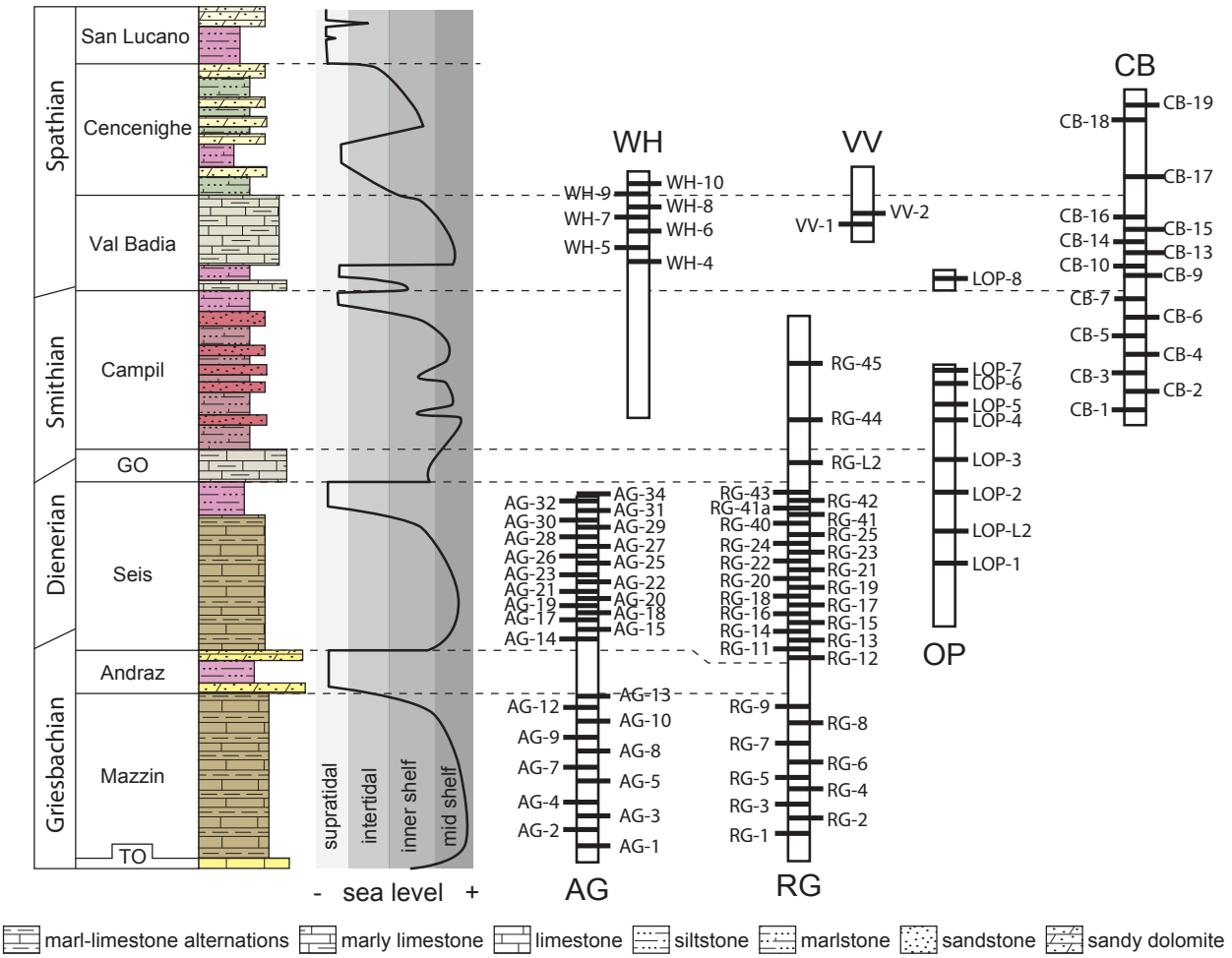

Fig. 2. General lithostratigraphy of the Werfen Formation. Sea level after (Broglio-Loriga et al. 1983). Range of the logged sections and stratigraphic relationship of sampled intervals. TO - Tesoro Oolith, GO - Gastropod Oolith, AG - Aferer Geisler, RG - Rosengarten, OP - L'Om Picol, CB - Costabella, WH - Weißhorn, VV - Val Venegia.

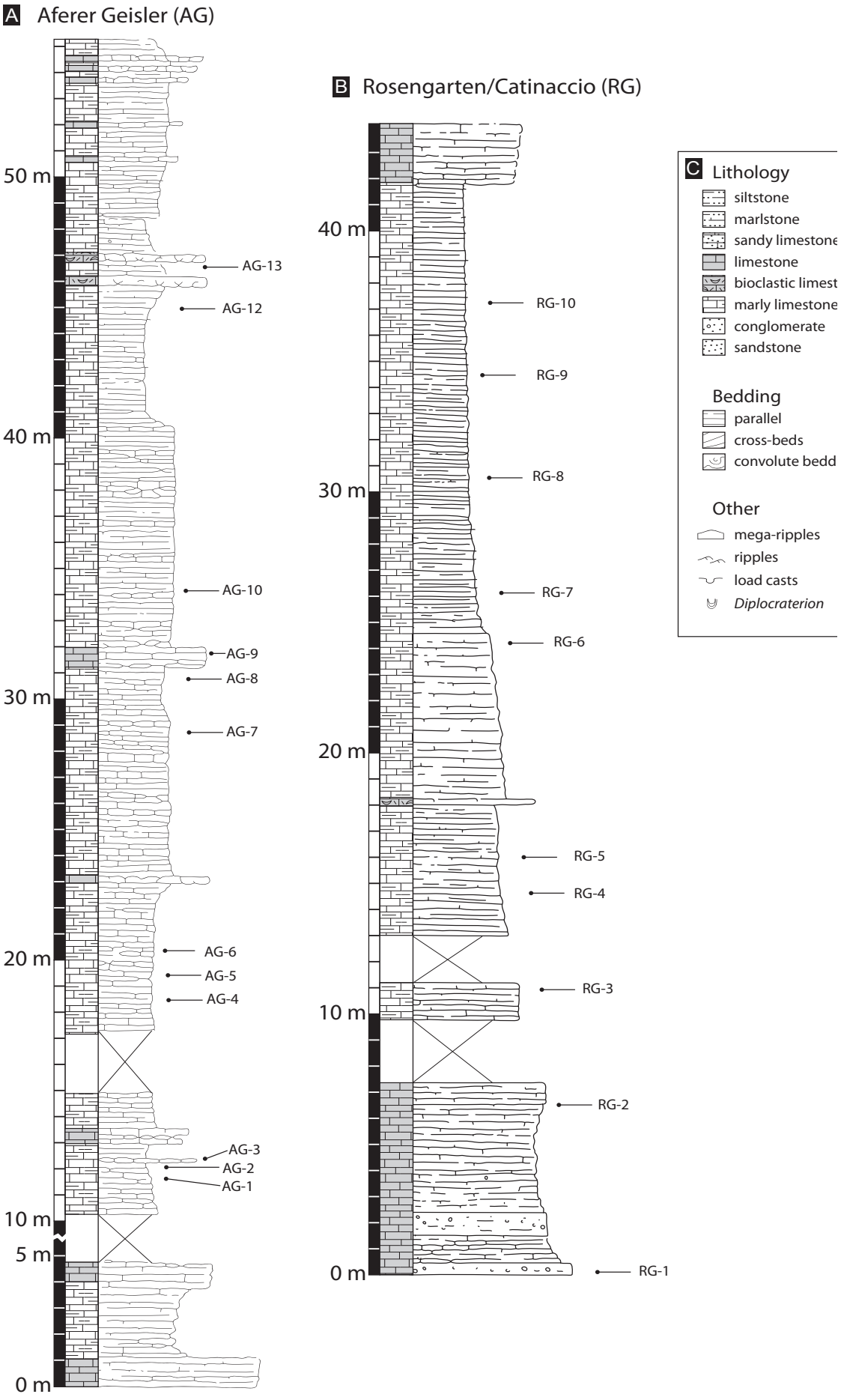

Fig. 3. Measured sections of the Mazzin Member at the Aferer Geisler (A) and the Rosengarten/Catinaccio (B). C, Legend for all sections (Figs. 4, 6, 7, 8)

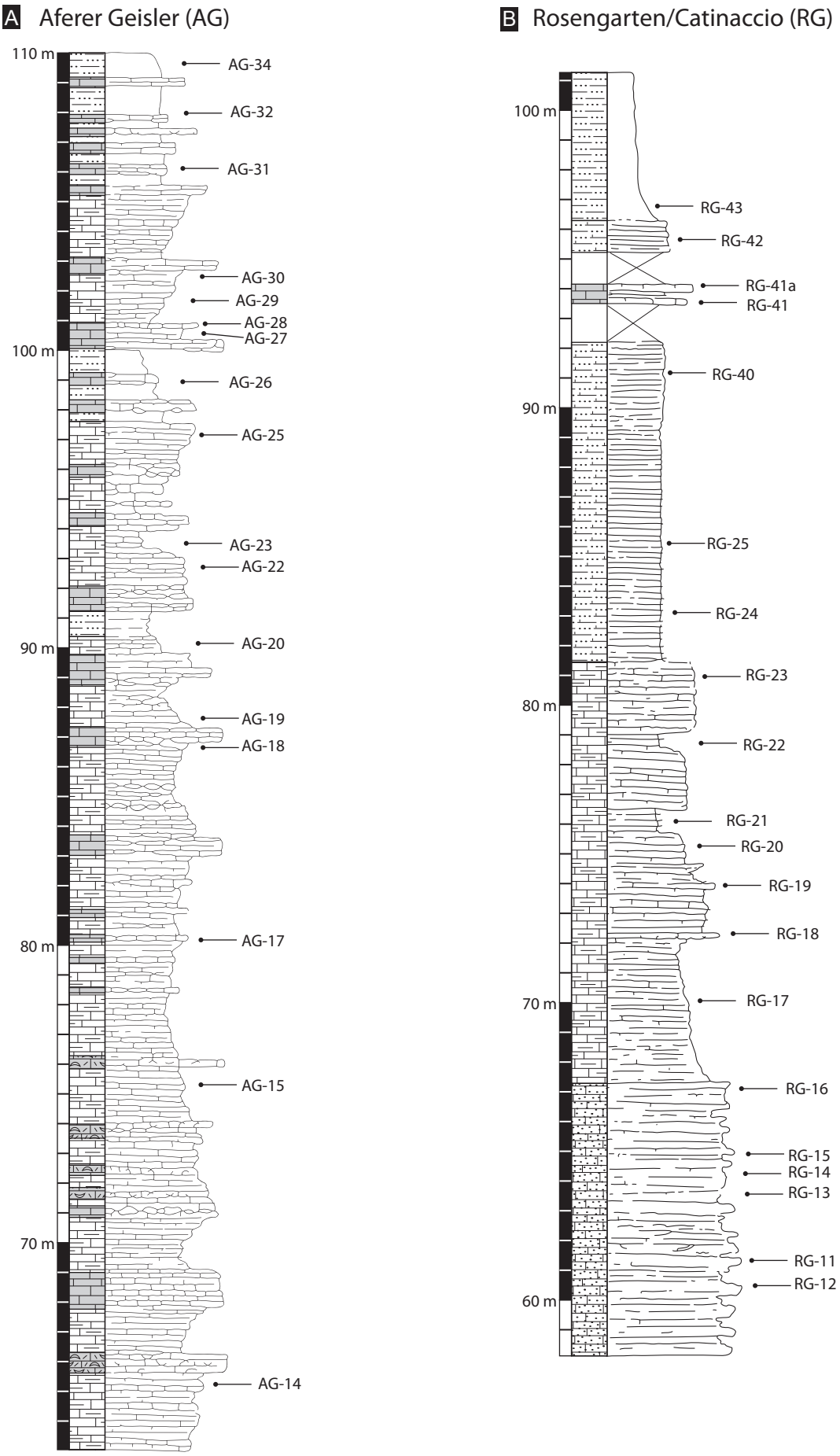

Fig. 4. Measured sections of the Seis/Siusi Member at the Aferer Geisler (A) and the Rosengarten/Catinaccio (B).

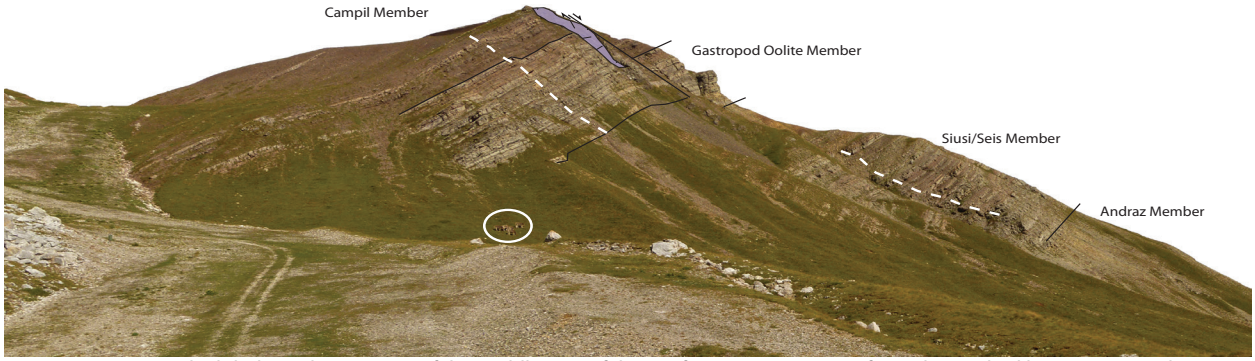

Fig. 5. Overview on the lithological succession of the 'middle' part of the Werfen Formation (cows for scale). Dashed line represents the measured section shown in Fig. 6. The yellowish strata between the Seis/Siusi- and the Gastropod Oolite Member represent the supratidal level that is herein regarded as part of the Seis/Siusi Member.

of association) is given as number of species.

Stratigraphic and depositional setting of the Werfen Formation

In the Dolomite region, the Werfen Formation is represented by an up to 500 m thick succession of mixed carbonate-siliclastic marine rocks (Broglio Loriga *et al*. 1983) deposited in western end of tropical Tethys (Fig. 1B). Broglio Loriga *et al*. (1983) established a lithostratigraphic subdivision, which found broad agreement (e.g. Neri and Posenato 1985; Broglio Loriga *et al*. 1990; Twitchett and Wignall 1996, Posenato 2008, Hofmann *et al*. 2011). The included units (as used in Posenato 2008, see also Fig. 2) are, in ascending order,: the Tesero Member, the Mazzin Member, the Andraz Horizon, the Seis/Siusi Member, the Gastropod Oolite Member, the Campil Member, the Val Badia Member, the Cencenighe Member, and the San Lucano Member. Due to highly diachronous facies development around the Permian Triassic transition, the extinction horizon is recorded within the Bulla Member of the underlying Bellerophon Formation (Posenato 2009) or the Tesero Member (Noé and Buggisch 1994; Wignall and Hallam 1992), respectively. Accordingly, the first occurrence of index fossil of the Permian-Triassic boundary *Hindeodus parvus*, is observed in the Tesero Member (Posenato 2009) or the Mazzin Member (Wignall *et al.* 1996). In all the sections considered herein, first clear post-extinction faunas, which are the focus of this study, commence to occur in the lower Mazzin Member. The Mazzin Member (Fig. 3) is about 50 m thick and is generally composed of laminated marl and mudstone intercalated with bioclastic packstone (Broglio Loriga *et al*. 1983; own observation). This facies suggests a subtidal setting below the fair-weather wave base, periodically affected by storm events (Broglio Loriga *et al*. 1983; 1990), and is, thus, indicative of a distal mid-shelf position. Conodont biostratigraphy (Perri 1991) suggests that the major part of the Mazzin Member is Griesbachian in age with its top possibly ranging into the basal Dienerian. However, Perri (1991) noted that this part of the Werfen Formation is devoid of age-diagnostic conodonts with respect to globally recognised zones. Posenato (2009) placed the Mazzin Member entirely into the Griesbachian. The overlying Andraz Horizon is up to 25 metre thick and composed of reddish siltstones and yellow dolostones interpreted as supratidal deposits (Broglio Loriga *et al*. 1983). It is generally poorly exposed and devoid of fossils. The succeeding Seis/Siusi Member (Figs. 4, 5) is about 50 metres thick and in its basal part (Unit A in Broglio Loriga *et al*. 1990) composed of sandy limestone, packstone, and bioclastic grainstone. This succession is interpreted as transgressive sequence mainly recording mid-shelf conditions. The overlying part is generally much more fine-grained and records a distal mid-shelf facies with only rare storm influence (Unit B in Broglio Loriga *et al.* 1990, own observation). The succeeding interval, recognised as unit C in Broglio Loriga *et al*. (1990), is composed of reddish marls and mudstone that are intercalated with bioclastic grainstones, which show a generally shallowing-upward trend upsection (Broglio Loriga *et al.* 1990). Some microgastopod-rich packstones are frequently observed in this unit and the distinction to the Gastropod Oolite Member may be difficult (see below) if the whole succession is not continuously exposed (but see Fig. 5). The succeeding interval (Unit D in Broglio Loriga *et al.* 1990) is composed of calcareous sandstone intercalated with reddish marls. Sandstone beds showing hummocky-cross stratification as well as ripple-cross lamination are more frequent in this upper part of the Siusi Member. This is interpreted as a generally shallowing-upward trend by Broglio Loriga *et al.* (1990), which is supported by our observations.

This unit is overlain by an up to 25 metre thick inter- to supratidal succession (Fig. 5) which has been subject to some discussion. Broglio Loriga *et al.* (1983) included this level first in the Siusi Member and later (Broglio Loriga *et al*. 1990) in the Gastropod Oolite Member. However, this supratidal horizon is very poorly exposed in all sections observed herein, whereas the Gastropod Oolite Member Unit B (figure 6 in Broglio Loriga *et al.* 1990 and accompanying text) is always developed as cliff-forming unit (Fig. 5) that is easily recognised in the field. Furthermore, the transgressive character of this "Unit B" would also represent a more intuitive lithostratigraphic distinction between both Members. We thus follow Broglio Loriga *et al.* (1983) and restrict the Gastropod Oolite Member to this unit only.

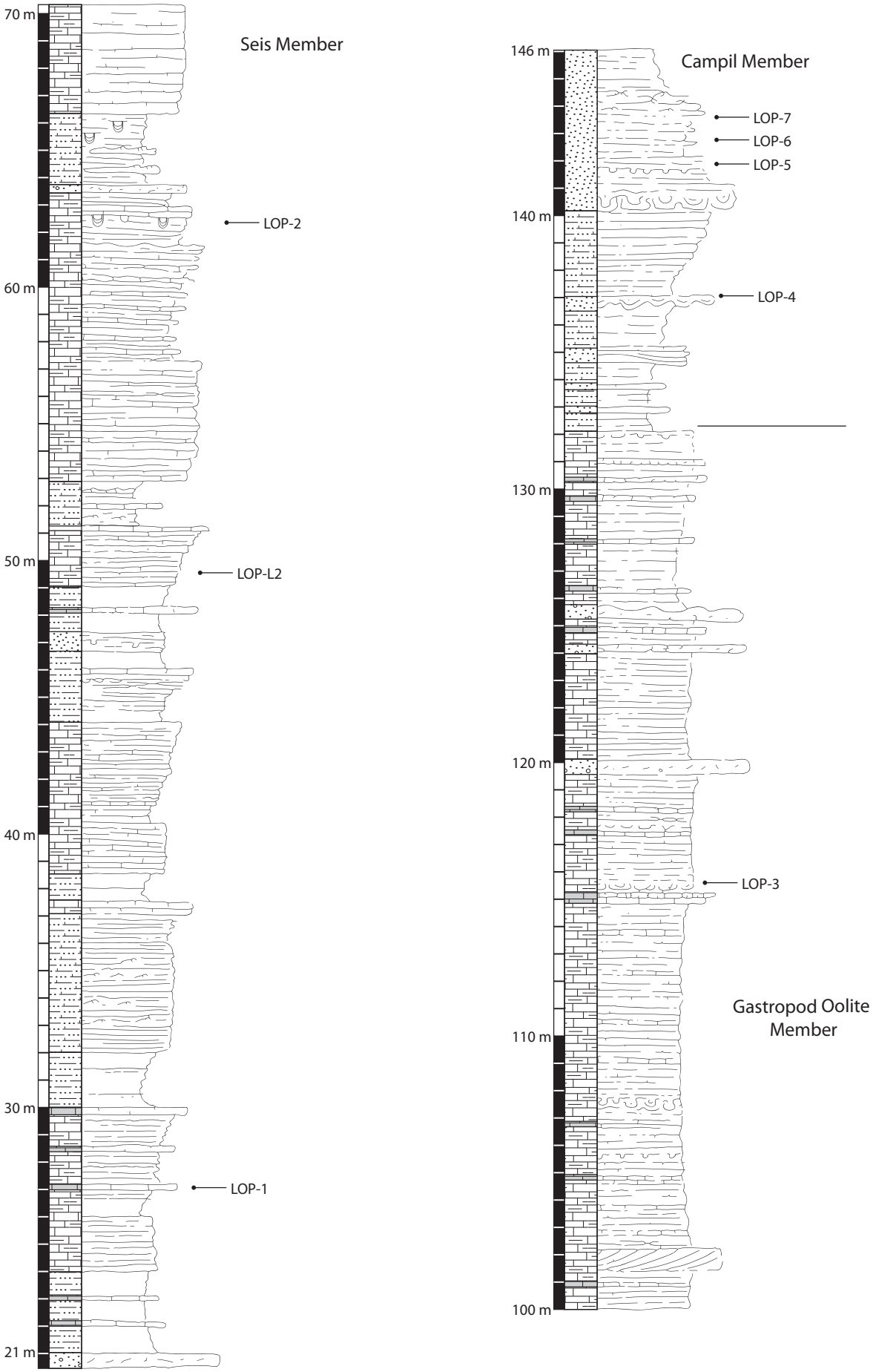

Fig. 6. Measured section of the Werfen Formation at the L'Om Picol locality.

Based on extensive review of available biostratigraphic and chemostratigraphic data, Posenato (2008) placed the Dienerian-Smithian boundary within the lower part of the Gastropod Oolite.

The Gastropod Oolite Member (Figs 5, 6) is usually 20 to 30 metres thick and is mainly composed of parallel-bedded greyish and reddish calcareous sandstone, marl as well as sandy mudstone. Most recognisable features of this unit are numerous purple to pinkish bioclastic grainstones with abundant microgastropods. These beds frequently show mega-ripple bedforms. Furthermore characteristic is the presence of reddish to pinkish dm-thick limestone-breccia. This unit is trangsressive at its base and records conditions repeatedly fluctuating between inner and mid-shelf environments that were frequently disturbed by high-energy events. In the upper part, brownish and reddish siltstone become more frequently intercalated, which is interpreted as a deepening trend. The transition to the overlying Campil Member is gradual (Fig. 5). The cessation of carbonate deposition is herein regarded as the most valuable field criterion to mark the base of the Campil Member.

The Campil Member (Fig. 7) attains a thickness of about 100 metres and is dominantly composed of reddish siltstone and sandstone with very few bioclastic limestone inctercalations. Most notable sedimentary features are thick sheets of sandstone with convolute bedding and ball and pillow-structures, which indicate high sedimentation rates. Also frequently observed are hummocky cross-bedded and ripple-cross laminated sandstones. All these feature suggest deposition in a storm- and wave-dominated setting of a mid- and, to a lesser extend, inner shelf setting. Marker beds with stratigraphic importance are scarce. The occurrence of the bivalve *Costatoria subrotunda* is recognised as marker (see Posenato 2008, and references therein) for the late Smithian. However, fossiliferous levels are very rare in this unit, which impedes usability of this stratigraphic indicator.

The transition to the overlying Val Badia Member (Fig. 8) is marked by a supratidal horizon, which was included this in the Val Badia Member by Broglio Loriga *et al*. (1990), analogue to their treatment of the supratidal horizon at the transition between the Seis/Siusi and the Gastropod Oolite Member (see above). However, for the same reasons outlined above, which are (i) the good exposure and (ii) the clear transgressive character of the first marine Val Badia lithotypes, we place the base of the Val Badia Member at the first limestone bed of the Val Badia "Unit B" of Broglio Loriga *et al.* (1990). A less extensive (up to 10 metres thick) supratidal horizon occurs above "Unit B", yet the remainder of the Val Badia Member is composed of marly mudstone, bioclastic grainstone and packstone as well as some calcareous sandstone beds. It is generally interpreted as a distal mid-shelf succession, which shows a general shallowing-upward trend with hummocky cross-bedded and through cross-bedded sandstone at the top of the Member. The occurrence of *Tirolites cassianus* at the base of the

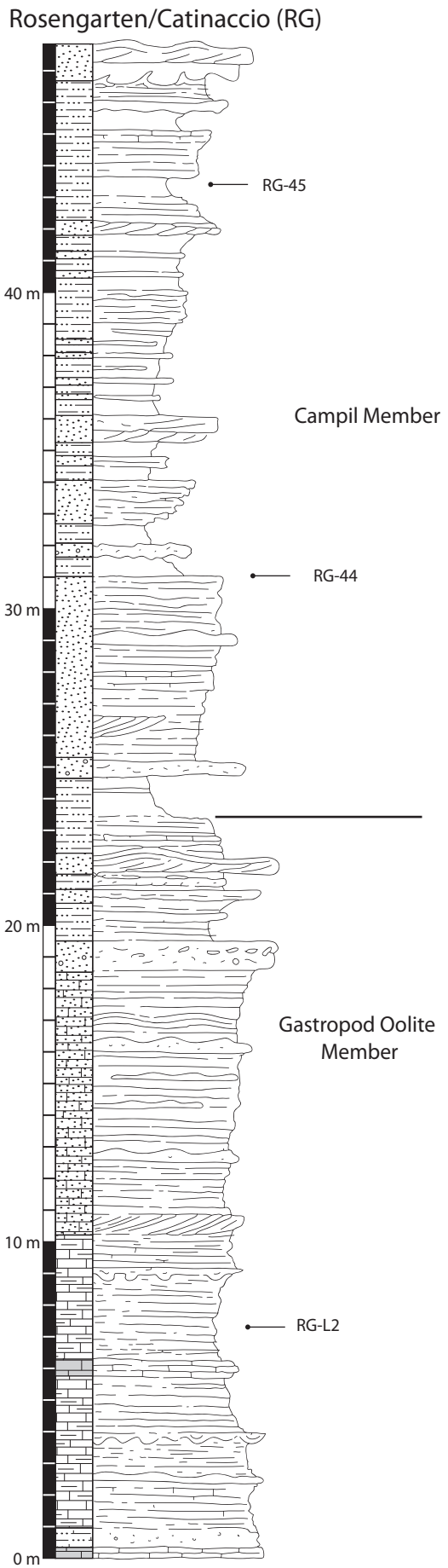

Fig. 7. Measured section of the Gastropod Oolite- and the Campil Member at the RosengartenL'Om Picol locality.

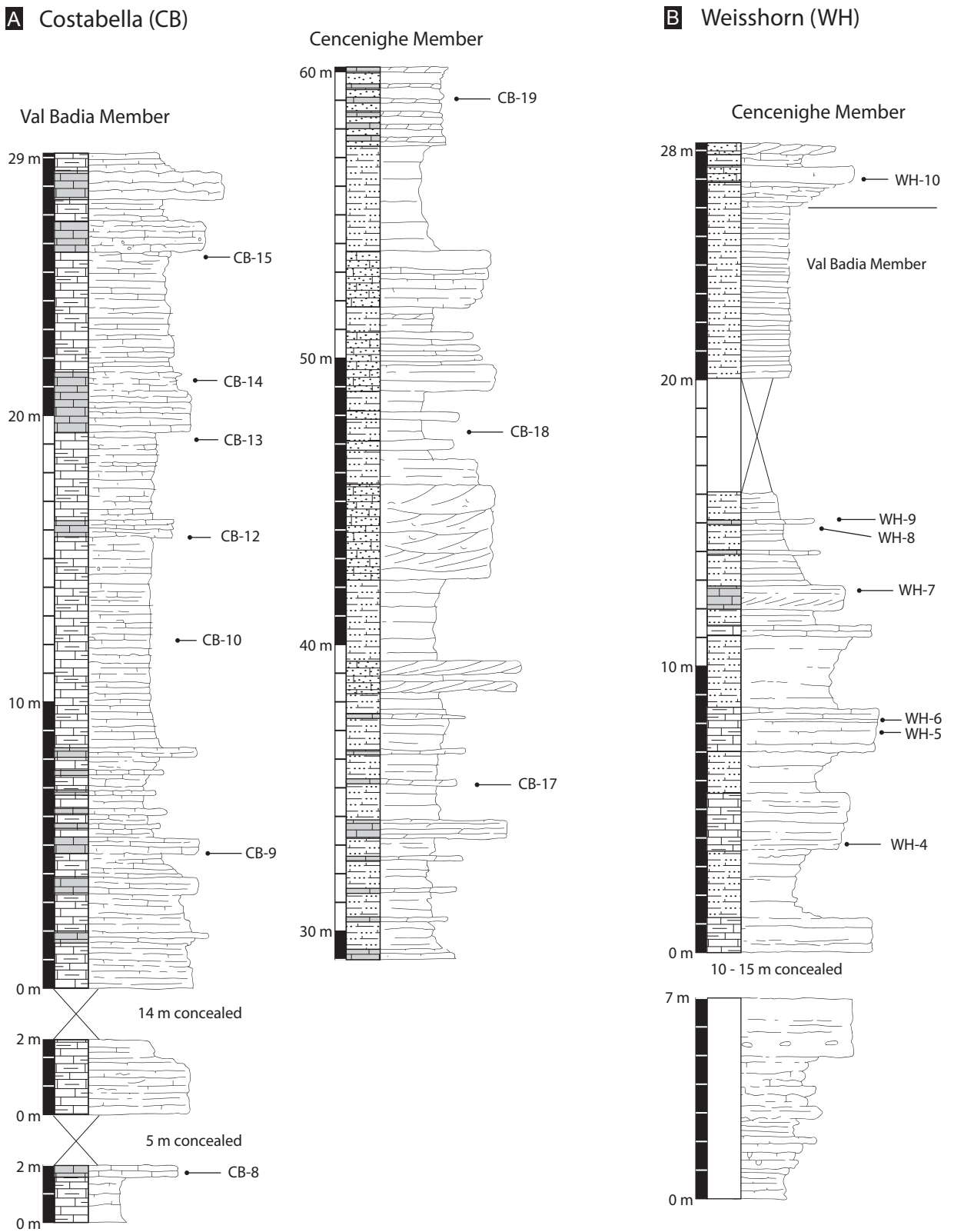

Fig. 8. Measured sections of the Val Badia and the Cencenighe Member at the Costabella (A) and the Weisshorn locality (B).

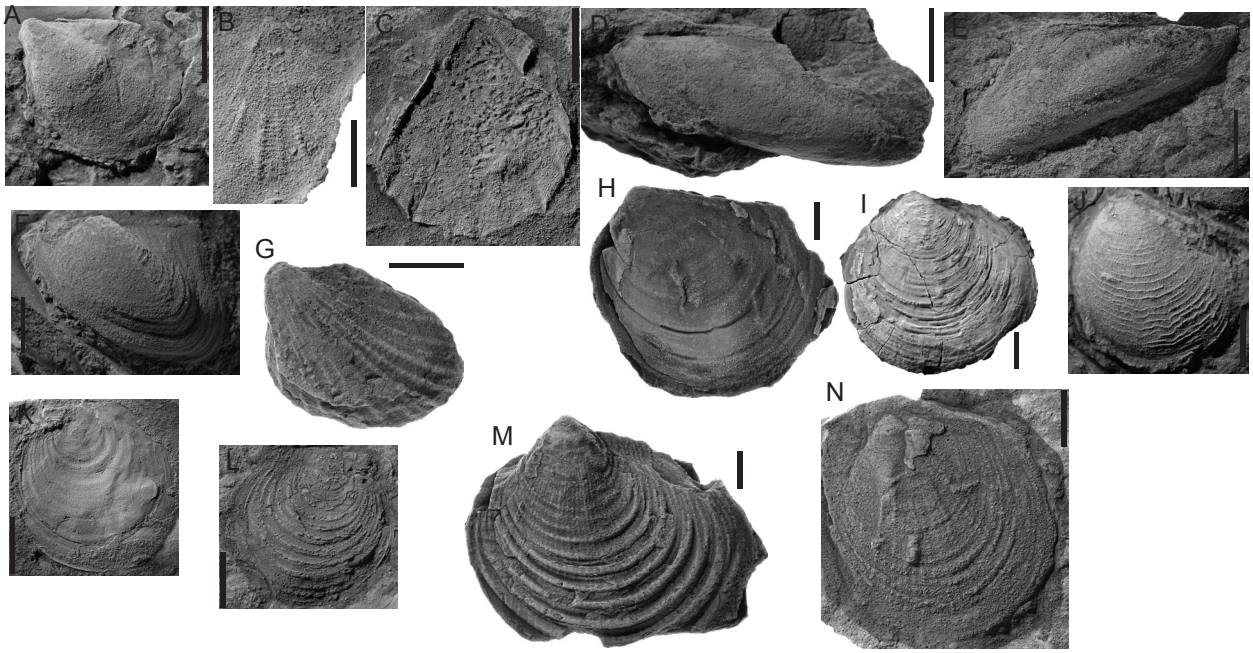

Fig. 9. Macrofossils of the Werfen Formation. All scales represent 5 mm if not indicated otherwise. A, *Pteria* cf. *ussurica,* left valve, AG-22, (20130620-64). B, *Avichlamys voelseckhofensis,* left valve, Val Badia Member float on section CB (20130616-21), scale = 3 mm. C, *Avichlamys voelseckhofensis,* left valve, Val Badia Member float on section CB (20130616-22). D, *Bakevellia albertii,* left valve, WH-8 (20130620-62). E, *Bakevellia albertii,* right valve, VV-2 (20130620-61). F, *Bakevellia exporrecta,* left valve, VV-2 (20130620-50). G, *Towapteria scythica,* left valve, RG-1 (20130620-62). H - L, *Claraia aurita.* H, left valve, AG-23 (20130616-06). I, left valve, left valve, AG-29 (20130616-01). J, left valve, AG-8, (20130620-75). K, right valve, float from the lower Mazzin Member AG (20130616-18). L, right valve, float from the lower Mazzin Member AG (20130616-17). M, *Claraia clarai*, left valve, AG-15, (20130616-07). N, *Claraia clarai*, left valve, AG-15, (20130616-15).

Member suggests an Early Spathian age.

The overlying Cencenighe Member (Fig. 8) is heterogeneous in terms of facies and lateral relationships. It is mainly composed of yellowish calcareous sandstone, pinkish and olive-grey oolithic grainstone as well as reddish and brown siltstone. Highly fossiliferous calcareous sandstones contain oolites and some reworked shell material indicative of wave dominated environments. These beds represent inner and proximal mid-shelf deposits. The purely calcareous oolite bodies form repetitive, up to 0.5 metres thick sets of tabular and through cross-bedded packages showing alternating flow directions. Interbedded reddish siltstones are typically heterolithic. Both types of facies are highly indicative for tidal influence. Broglio Loriga *et al.* (1990) also suggested that the main part of the Cencenighe Member represents fining upward cycles with lower intertidal and shallow subtidal oolite tidal bars that are overlain by mid to upper intertidal mudflats represented by the siltstone facies. Our observations largely supports this interpretation.

The overlying San Lucano Member is about 25 metres thick in the study area and is generally composed of yellow dolostone and reddish siltstone which have also been interpreted as intertidal and supratidal deposits (Broglio Loriga *et al.* 1990). Our survey of this Member did not yield any fossil material.

Benthic associations of the Werfen Formation

General Remarks

The Faunas of the Werfen Formation is dominated by shallow infaunal, epibyssate and endobyssate suspension feeders (mainly bivalves) as well as epifaunal grazers (gastropods). Rarely observed are free lying suspension feeders (such as *Scythentolium*). Ophiuroids, which are epifaunal carnivores or detritus feeders, were very rarely observed. This adds up to six out of 13 typically Mesozoic benthic guilds (cf. Aberhan 1994). Faunal associations were obtained by Q-mode cluster analysis, which groups individual samples based on the occurrence and abundance of taxa within the data set. All associations recognised in the respective lithostratigraphic units, which roughly represent Early Triassic substages, are reviewed in the following. All macrofossils are identified on species level and are depicted in the Figures 9, 10 and 11.

Mazzin Member (Griesbachian Fig. 12)

Unionites fassaensis *association*. – This association (Fig. 13A) is represented by samples RG-1, RG-2, RG-3, RG-4, AG-1 AG-2 AG-3 and AG-4 and is, thus, exclusively recorded in the lower part of the Mazzin Member. The trophic nucleus comprises the species *Unionites fassaensis* only. *Pteria* cf. *ussurica*, *Coelostylina werfensis*, and Bellerophontid sp. A are also commonly observed. All other species (*Eumorphotis* sp. A, *Eumorphotis multiformis*, *Towapteria scythica*, *Claraia aurita*, *Neoschizodus orbicularis*, *Neoschizodus laevigatus*, and *Lingula tenuissima*) are rarely recorded. Species richness ranges from 2 to 7 (average 3.88). Overall species richness is 9. Dominace (D) values range from 0.33 to 0.98 (average 0.57).

The ecological spectrum comprises attached epifaunal (four species), attached semi-infaunal (one species) and shallow infaunal (four species) suspension feeders as well as epifaunal grazers (two species). In terms of

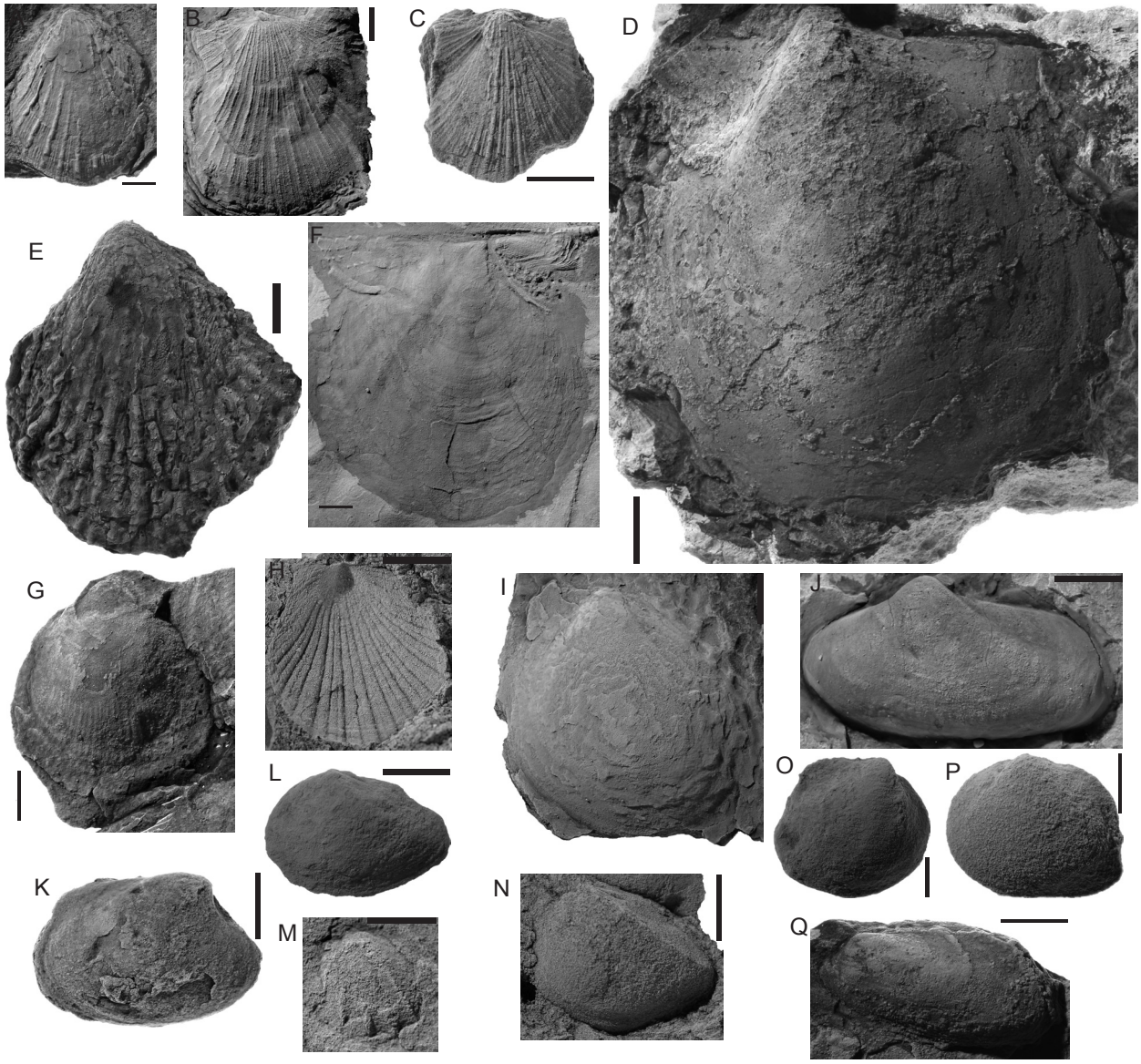

Fig. 10. Macrofossils of the Werfen Formation. All scales represent 5 mm if not indicated otherwise. A, *Eumorphotis beneckei,* left valve, float Campil Member, Rosengarten locality, (20130616-03). B, *Eumorphotis multiformis,* left valve, AG-23 (20130616-04), scale = 3 mm. C, *Eumorphotis multiformis,* left valve, AG-23 (20130616-11). D, *Eumorphotis telleri,* left valve, WH-10 (20130620-60), scale = 10 mm. E, *Eumorphotis tenuistriata,* left valve, WH-8 (20130616-09). F, *Eumorphotis telleri,* right valve, float from the Val Badia Member, Weisshorn (20130626-05), G, *Eumorphotis* sp. A, left valve, AG-17 (20130620-51). H, *Leptochondria albertii,* left valve, WH-10 (20130616-24). I, *Scythentolium* sp. A, left valve, WH-5 (20130616-24). J, *Unionites canalensis*, left valve, AG-29 (20130616-02). J, *Unionites fassaensis*, right valve, AG-23 (20130616-13). L, *Neoschizodus laevigatus*, left valve, LOP-8 (20130616-13X). M, *Costatoria subrotunda,* left valve, WH-5 (20130616-20). N, *Neoschizodus laevigatus*, left valve, VV-2 (20130616-13Y). O, *Neoschizodus orbicularis*, left valve, AG-12 (20130620-80), scale = 2 mm. P, *Neoschizodus orbicularis*, left valve, AG-12 (20130620-81), scale = 3 mm. P, *Stutchburia* sp. A, left valve, RG-25 (20130620-70).

absolute abundance of guilds, the spectrum is clearly dominated by shallow infaunal suspension feeders. The rarefaction curve indicates that further sampling would not have significantly increased species richness of this association.

Claraia aurita *association*. – The *Claraia aurita* association (Fig. 13C) comprises the samples AG-5, AG-7, AG-8, AG-13, RG-5, RG-6, RG-7, RG-8, and RG-9, which represent mainly the middle and upper portion of the Mazzin Member. *Claraia aurita* is the only species constituting the trophic nucleus. Also common is *Towapteria scythica.* All other species (Fig. 13C) are very rarely recorded. Species richness ranges from 1 to 9 (average 3.22). Cumulative species richness is 11. D ranges from 0.5 to 1 (average 0.71). Recorded ecological guilds are attached epifaunal (three species), attached semi-infaunal (one species) and shallow infaunal (five species) suspension feeders as well as epifaunal grazers (two species). The absolute guild abundance shows that attached epifaunal suspension feeders clearly dominate this association. The rarefaction curve suggests that recovered richness reflects the true diversity quite well.

Neoschizodus orbicularis *association*. – This association (Fig. 13B) comprises the samples AG-9 and AG-12. The trophic nucleus is represented by the species *Neoschizodus orbicularis, Claraia aurita,* and *Neoschizodus laevigatus.* Additonally recorded are *Lingula tenuissima*, *Coelostylina werfensis*, *Unionites fassaensis*, *Towapteria*

scythica, and *Eumorphotis multiformis*. The species richness of the samples is 6 and 7 (average 6.5) ant that of the association is 8. D-values range between 0.43 and 0.36 (average 0.4). The ecological guilds are attached epifaunal (three species) and shallow infaunal (five species) suspension feeders as well as epifaunal grazers (two species). Infaunal suspension feeders dominate in terms of numerical abundance. The rarefaction curve indicates a slightly insufficient sampling.

Seis/Siusi Member (?late Griesbachian – late Dienerian, Fig. 14)

Coelostylina werfensis *association*. – This association (Fig. 15A) comprises the samples AG-18, AG-20, AG-22, RG-41,RG-41a, RG-42, RG-43, RG-20, and RG-21. It is, thus, restricted to the middle and upper part of the Seis/ Siusi Member. The trophic nucleus contains the species *Coelostylina werfensis*, *Claraia aurita,* and *Claraia clarai.* Also common are *Unionites canalensis*, and *Unionites fassaensis*. Rarely observed are the species *Neoschizodus orbicularis, Neoschizodus elongatus,Pteria* cf. *ussurica*, *Eumorphotis multiformis*, and Bellerophontoid sp. A. The species richness ranges from 2 to 6 (average 4.3).

D-values range between 0.29 and 0.85 (average 0.51). The ecological guild spectrum involves attached epifaunal (three species), attached semi-infaunal (one species), shallow infaunal (four species) suspension feeders as well as epifaunal grazers (two species). The absolute guild abundance suggests that epifaunal grazers dominate

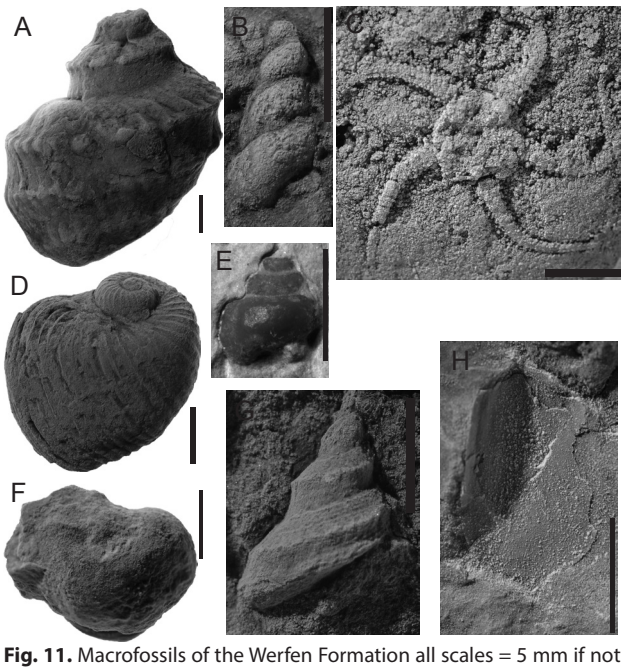

Fig. 11. Macrofossils of the Werfen Formation all scales = 5 mm if not otherwise indicated. A, *Werfenella rectocostata*, float Val Badia Member, Costabella locality, (20130620-54). B, *Coelostylina werfensis,* float upper Seis/Siusi Member, Aferer Geisler locality (20130620-55), C, *Praeaplocoma hessi*, WH-10 (20130616-14). D, *Natiria costata*, float Val Badia Member, Costabella locality, (20130620-58). D, *Pseudomurchisonia kokeni*, AG-29 (20130827-1), scale = 1 mm. E, *Eumorphotis tenuistriata*, left valve, WH-8 (20130616-09). F, Bellerophontid sp. A, AG-2, (20130620-56), scale = 3 mm. G, *Worthenia* sp. A, left valve, VV-2 (20130620-53). H, *Lingula tenuissima* , ventral valve, AG-9 (20130620-77).

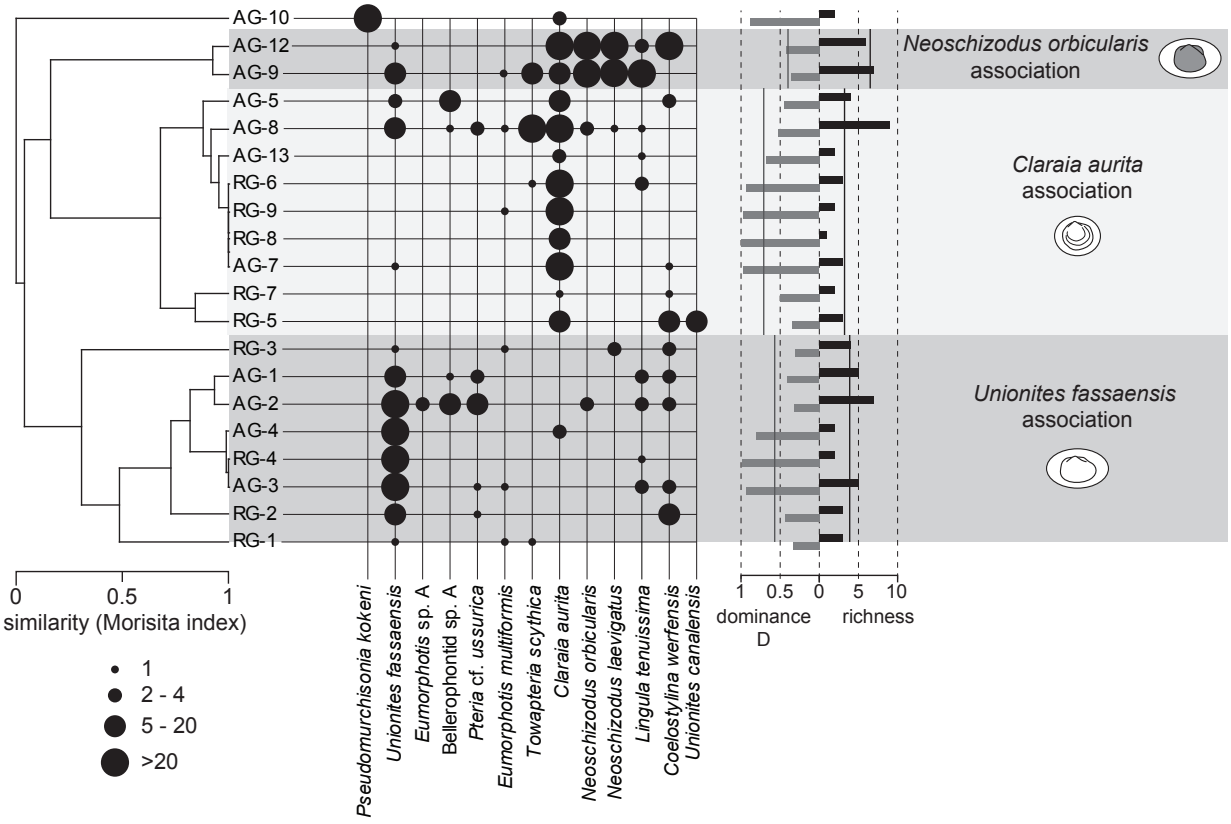

Fig. 12. Q-mode cluster analysis of the benthic faunas of the Mazzin Member.

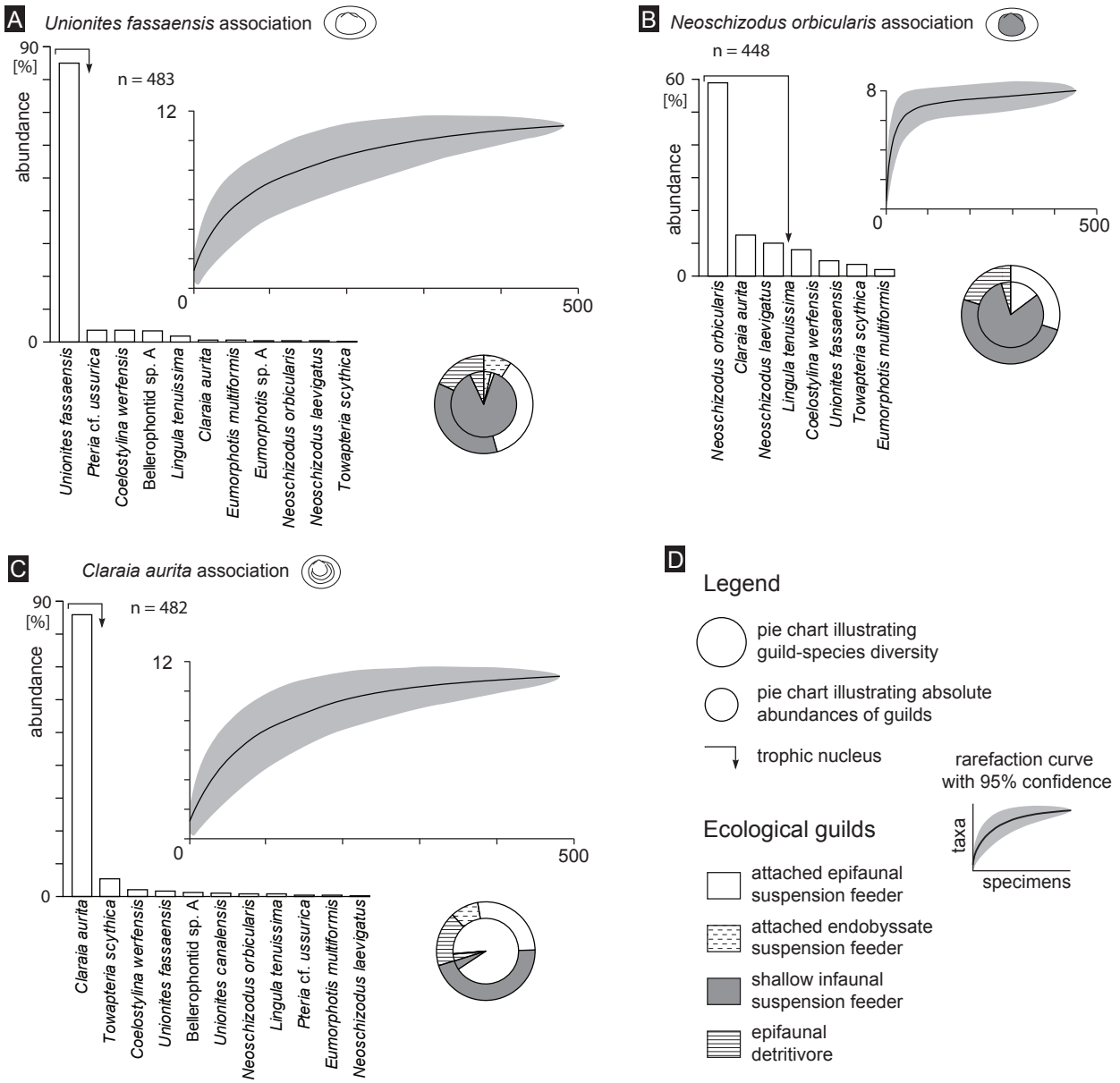

Fig. 13. Benthic association of the Mazzin Member. A, *Unionites fassaensis* association. B, *Claria aurita* association. C, *Neoschizodus orbicularis* association. D, Legend.

this association. The rarefaction curve shows that this association is somewhat undersampled.

Unionites canalensis *association*. – This association (Fig. 15B) is essentially observed throughout the whole Member. (samples LOP-2, AG-19, AG-23, AG-27, AG-30, AG-31, AG-32, RG-13, RG-14, RG-16, RG-17, RG-18, RG-22, RG-23, RG-24 and RG-40). The trophic nucleus comprises the species *Unionites fassaensis, Claraia aurita* and *Unionites canalensis*. Other common species are *Neoschizodus orbicularis*, *Claraia clarai*, *Coelostylina werfensis, Pteria* cf. *ussurica, Eumorphotis multiformis,* and *Neoschizodus laevigatus.* Rarely recorded are *Neoschizodus elongatus* and *Eumorphotis* cf. *hinnitidea*. The species richness ranges from 2 to 7 (average 3.75). Cumulative association richness is 11. D-values range between 0.19 and 0.80 (average 0.43). Present ecological guilds are attached epifaunal (four species), attached semi-infaunal (one species) and shallow infaunal (five species) suspension feeders as well as epifaunal grazers (one species). Attached epifaunal and shallow infaunal suspension feeders equally dominate the absolute abundance spectrum. The rarefaction curve indicates that this association reproduces well the true diversity.

Pseudomurchisonia kokeni *association*. – The *Pseudomurchisonia kokeni* association (Fig. 15D) is composed of the samples RG-25, AG-28, and AG-29. All these samples come from the upper Seis/Siusi Member and represent the conspicuous "Gastropod Oolite" facies. *Pseudomurchisonia kokeni* and *Claraia aurita* constitute the trophic nucleus. *Unionites canalensis* and *Neoschizodus elongatus* may be also common. *Stutchburia* sp. A and *Eumorphotis multiformis* is rarely observed. Species richness ranges from 1 to 5 (average 3.33) and

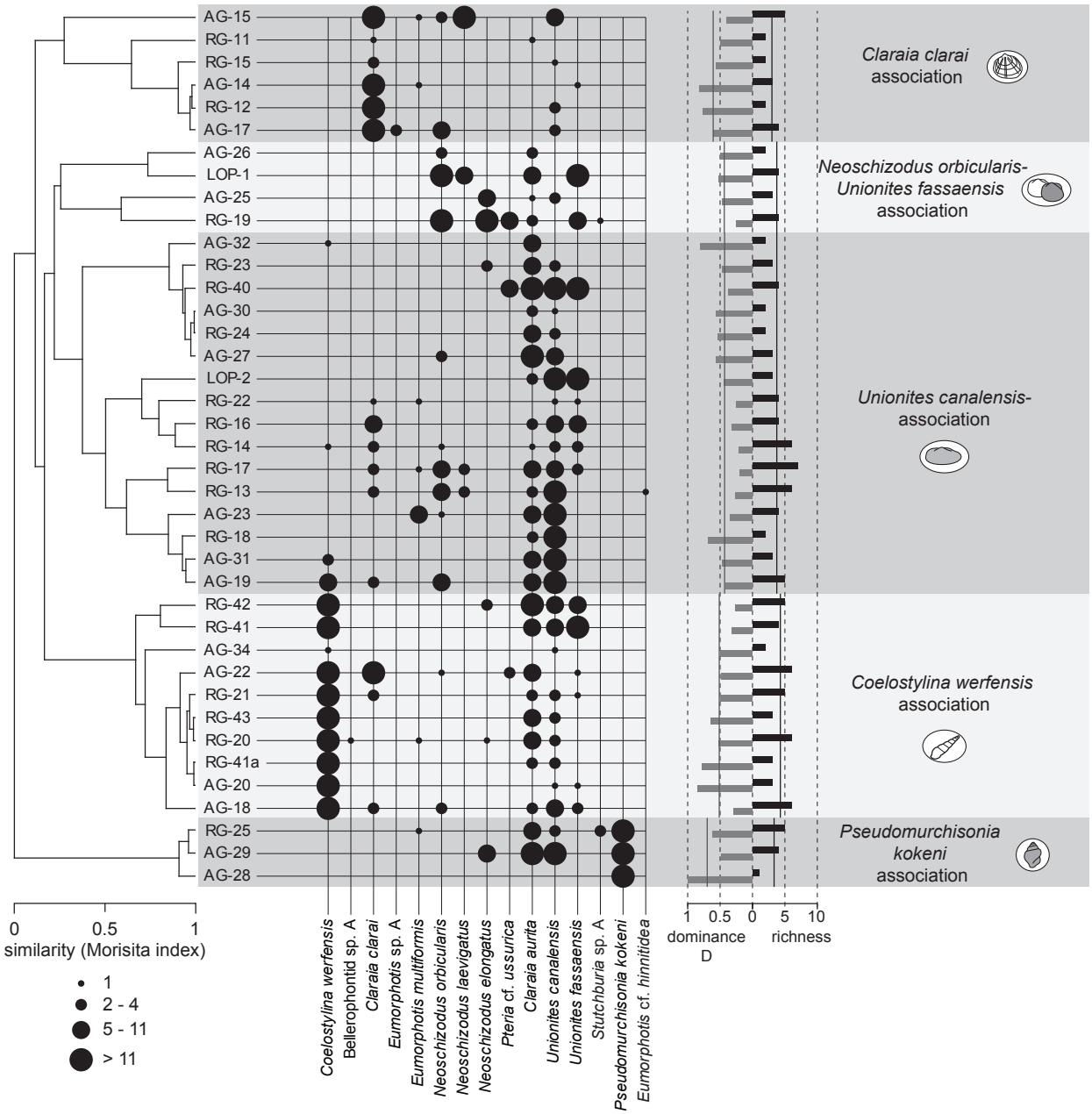

Fig. 14. Q-mode cluster analysis of the benthic faunas of the Seis/Siusi Member.

the total richness of the association is 6. D-values range between 0.47 and 1 (average 0.70). Recorded ecological guilds include attached epifaunal (two species) and shallow infaunal (three species) suspension feeders as well as epifaunal grazers (one species) with each being represented by four species. Epifaunal grazers dominate with about three forth the absolute abundance of guilds. The rarefaction curve suggests that this association is well sampled.

Neoschizodus orbicularis-Unionites fassaensis *association*. – This association (Fig. 15E) is recorded by the samples AG-25, AG-26, LOP-1, and RG-19. It thus tends to occur also in the middle and upper Seis/Siusi Member. The trophic nucleus includes the species *Neoschizodus orbicularis, Unionites fassaensis* and *Neoschizodus elongatus. Claraia aurita, Neoschizodus laevigatus* and *Pteria* cf. *ussurica* are commonly observed. The species *Unionites canalensis* and *Stutchburia* sp. A are rare. Species richness ranges from 2 to 6 (average 3.75) and the total richness of the association is 8. D-values range between 0.25 and 0.53 (average 0.44). Shallow infaunal (six species), attached semi-infaunal (one species) and attached epifaunal (one species) suspension feeders are recorded in this association, in which shallow infaunal suspension feeders also dominate in terms of absolute abundance. The rarefaction curve indicates that this association may be slightly undersampled.

Claraia clarai *association*. – The *Claraia claria* association (Fig. 15C) is composed of the samples AG-14, AG-15, AG-17, RG-11, RG-12, and RG-15, which

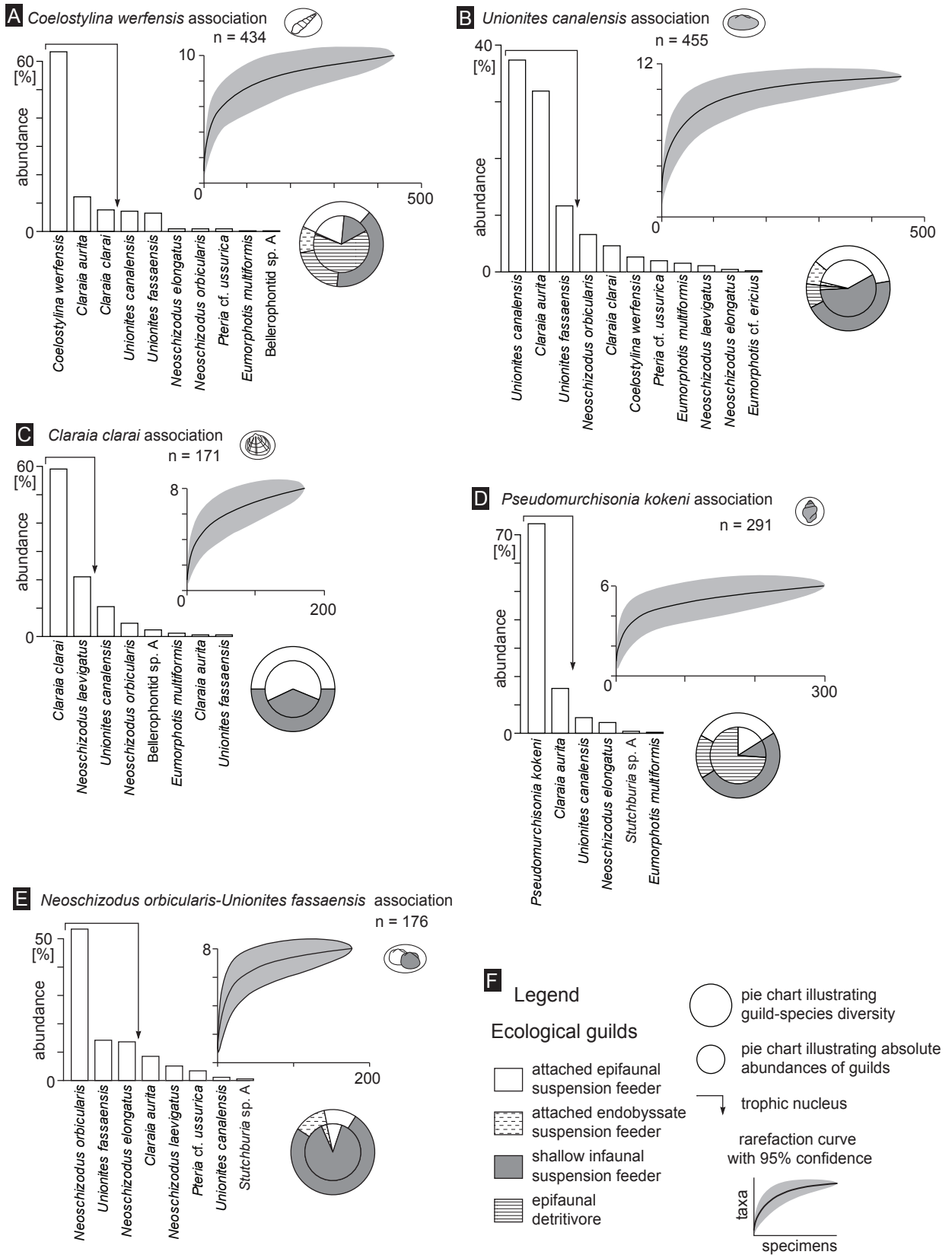

Fig. 15. Benthic association of the Mazzin Member. A, *Coelostylina werfensis* association. B, *Unionites canalensis* association. C, *Claraia clarai* association. D, *Pseudomurchisona kokeni* association. E, *Neoschizodus orbicularis-Unionites fassaensis* association F, Legend.

all were recovered from the lower Seis Member. The trophic nucleus comprises the species *Claraia clarai* and *Neoschizodus laevigatus*. Locally common are *Unionites canalensis, Neoschizodus orbicularis,* and Bellerophontoid sp. A. Rarely observed are *Eumorphotis multiformis*, *Claraia aurita*, and *Unionites fassaensis*. Species richness ranges from 2 to 5 (average 3) and the total richness of the association is 8. D-values range between 0.40 and 0.82 (average 0.61). The ecological guild spectrum includes attached epifaunal and attached shallow infaunal suspension feeders with each being represented by four species. In terms of absolute abundance both guilds are also almost equally abundant. The rarefaction curve shows that this association suffers from insufficient sampling.

Gastropod Oolite- and Campil Member

General remarks. – Macrofossil occurrences in the strata of the Gastopod Oolite Member and the Campil Member are rare. Given the few sample levels and the comparably low fossil abundance, a cluster analysis as carried out for the other time intervals was not performed for these samples. The ecological spectrum is, thus, obtained from the bulk composition of all samples. The most abundant species are *Unionites fassensis*, *Neoschizodus laevigatus,* and *Scythentolium* sp. A. *Unionites canalensis* can be locally abundant. Seldomly observed are *Bakevellia exporrecta*, *Eumorphotis* cf. *beneckei,* and *Eumorphotis multiformis*. Species richness ranges from 1 to 3 (average 1.8) and the total richness of the association is 7. D-values range between 0.44 and 1 (average 0.78). Ecological guilds include infaunal (three species), byssaly attached epifaunal (two species), free-lying epifaunal (one species) and semi-infaunal (one species) suspension feeders. In terms absolute abundance infaunal suspension feeders clearly dominate. Rarefaction indicates slightly incomplete sampling.

Val Badia- and Cencenighe Member (Spathian Fig. 16)

Natiria costata *association*. – This association (Fig. 17A) is recorded by the samples CB-14, CB-10, LOP-8, CB-13, WH-7, CB-9, VV-1, CB-17, and CB-16 and thus confined to the Val Badia Member. The trophic nucleus comprises the species *Natiria costata* and *Neoschizodus laevigatus*. Furthermore recorded are, in descending abundances, *Bakevellia exporrecta*, *Unionites fassaensis, Eumorphotis telleri, Werfenella rectocostata* and *Eumoprhotis* cf. *hinnitidea*. Species richness ranges from 1 to 5 (average 2.8) and the total richness of the association is 7. D-values range between 0.36 and 1 (average 0.52). Ecological guilds include infaunal and attached epifaunal suspension feeders as well as epifaunal grazers (two species each). One species of semi-infaunal suspension feeders is recorded. Epifaunal grazers dominate in terms of absolute abundances. Rarefaction indicates slightly insufficient sampling.

Bakevellia exporrecta *association*. – The *Bakevellia exporrecta* association (Fig. 17B) contains the samples WH-9, CB-19, CB-18, WH-10, VV-2, and WH-8 involving the Val Badia and Cencenighe Member. The species *Bakevellia exporrecta, Natiria costata, Neoschizodus laevigatus,* and *Eumorphotis telleri* constitute the trophic nucleus. *Leptochondria albertii, Werfenella rectocostata, Bakevellia albertii* are also common. Rare species include *Eumorphotis* cf. *hinnitidea, Unionites canalensis, Costatoria subrotunda, Eumorphotis multiformis, Unionites fassaensis, Worthenia* sp. A, and *Praeaplocoma hessi*. Species richness ranges from 2 to 8 (average 5.2) and the total richness of the association is 14. D-values range between 0.17 and 0.87 (average 0.44). Recorded ecological guilds are attached epifaunal

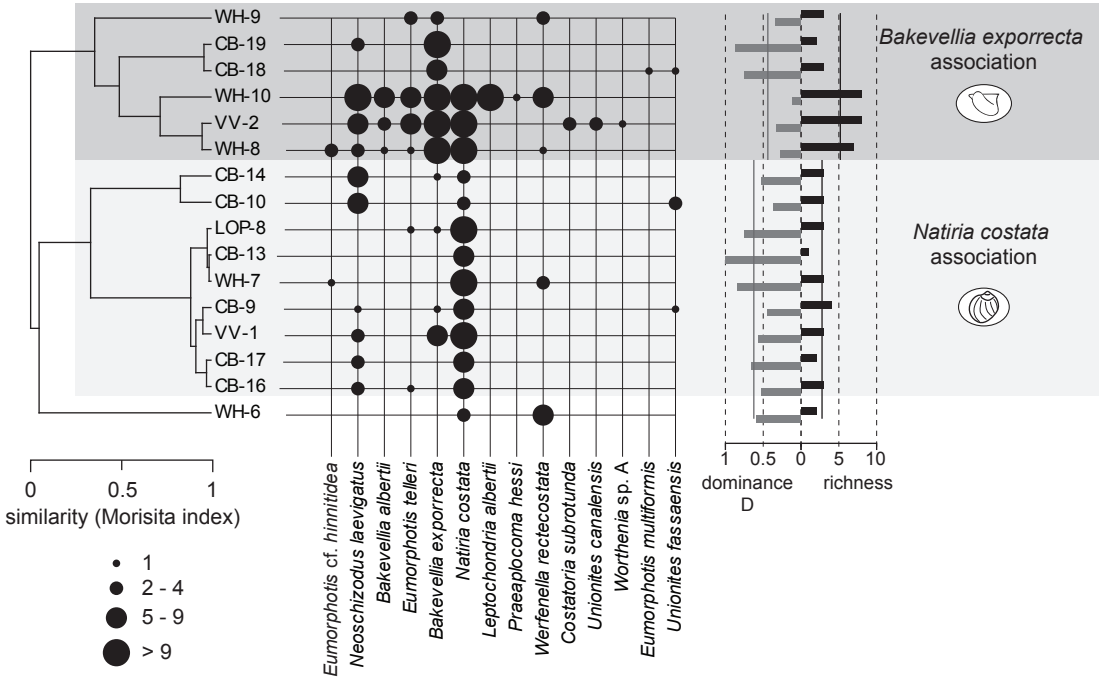

Fig. 16. Q-mode cluster analysis of the benthic faunas of the Val Badia and the Cencenighe Member.

(five species), attached semi-infaunal (two species) and infaunal (three species), as well as epifaunal grazers (three species). Epifaunal carnivores are recorded with one species. Numerically, attached epifaunal suspension feeders dominate with about 50%. Except for epifaunal carnivors, which play virtually no role, all other guilds contribute about equally to the remaining half. The rarefaction curve indicates significant under sampling.

Associations, diversity and ecological guild structure through time

In the Mazzin Member, the distribution of benthic associations follows a clear trend. Samples constituting the *Unionites fassaensis* association are found in the lowermost part of this unit. The *Claraia aurita* association is observed in the middle and upper part of the Mazzin Member. The *Neoschizodus orbicularis* association is recorded in the upper part of the Mazzin Member at the Aferer Geisler section. Accompanying sample richness and dominance values (Fig. 12) suggest that low diverse/ high dominance samples are concentrated within the *Claraia aurita* association. Although samples with similar values are also present in the other two associations, these show on average somewhat higher sample richness and lower dominance values. However, both sampled sections show no marked overall trend (Fig. 18) with respect to these two parameters. Only in the Aferer Geisler section, sample richness peaks within the middle to upper portion of the Mazzin Member.

The distribution of associations in the Seis/ Siusi Member shows no notable trend. Only the *Claraia clarai* association is clearly restricted to the lower part of the Member. This signal likely reflects the narrow stratigraphic range of *Claraia clarai*. All other associations are alternating throughout the sections. Furthermore, there exists no correlation with principle lithology (Figs. 4, 6) and the distribution of associations. The cluster analysis (Fig. 14) of Seis/Siusi samples shows that most associations are dominated by *Claraia aurita* and *Unionites canalensis*. The clusters and, hence, the associations mainly reflect the fluctuating presence of few occasionally dominating species, most notably *Coelostylina werfenensis* and *Pseudomurchisonia kokeni*. Thus, the principle species composition does not change with respect to sedimentary facies and time. However, there is an overall trend with increasing dominance values and decreasing sample richness towards the top of the Member (Fig. 18).

The whole Gastropod Oolite and Campil Member is characterised by low sample richness, association richness, and high dominance values (Fig. 18). Taxonomic composition and ecological structure is also rather uniform. The data from the Spathian Val Badia and Cencenighe Member indicate a rise in diversity and a decrease in dominance values (Fig. 18) when compared to the underlying Campil Member. The *Natiria costata* association is notably less diverse than the *Bakevellia exporrecta* association and is exclusively recorded in the Val Badia Member. The *Bakevellia exporrecta* association tends to occur in the upper Val Badia Member and some

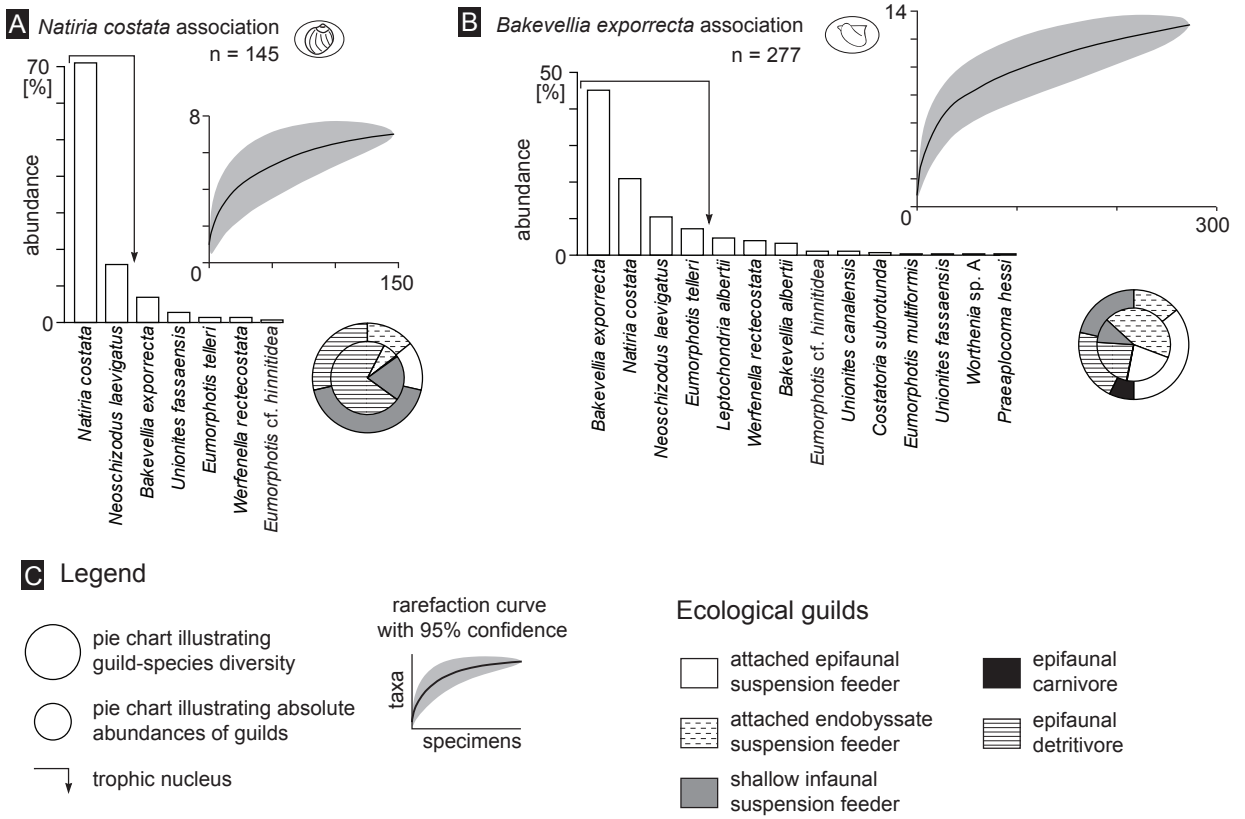

Fig. 17. Benthic association of the Val Badia and the Cencenighe Member. A, *Natiria costata* association. B, *Bakevellia exporrecta* association. C, Legend.

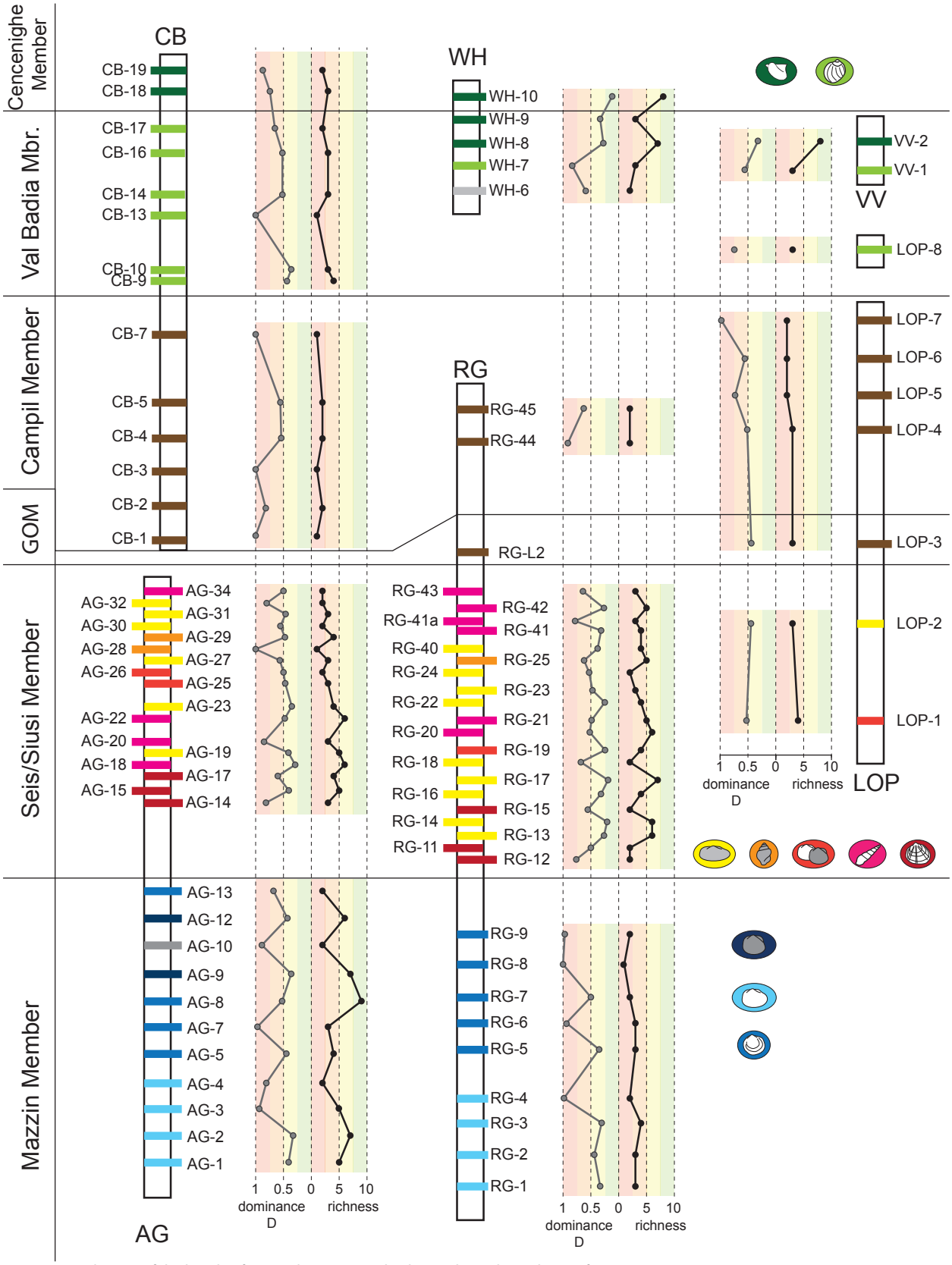

Fig. 18. Distribution of the benthic faunas, domiance and richness throughout the Werfen Formation.

levels of the generally poorly sampled Cencenighe Member.

Ecological guilds structure is relatively uniform throughout the Griesbachian and Dienerian part of the Werfen Formation (Fig. 19). Present guilds include shallow infaunal, semi-infaunal, epifaunal suspension feeder and epifaunal grazer. The only guild that is added in the Campil Member is that of free-lying epifaunal suspension feeders. Epifaunal ?carnivores (Ophiuroids) are first recorded in the Spathian Cencenighe Member. However, related trace fossils (*Asteriacites*) are frequently observed in the Smithian Campil Member already. In sum, there is no trend observed as all units are dominated by the same ecological guilds (Fig. 19).

Discussion

Although the Werfen Formation has always been in the focus of post-extinction studies, its macrofauna received comparably little attention. A number of recent studies (Nützel 2005; Nützel and Schulbert 2005; Posenato 2008; 2009; Metcalfe *et al.* 2011) in fact discussed aspects of the Werfen macrofauna with respect to the recovery, but a comprehensive reconstruction of benthic ecosystems was lacking. Hitherto published recovery studies from this palaeogeographic region rest exclusively on ichnological data (Twitchett and Wignall 1996; Hofmann *et al.* 2011). In the following, we review the ecological significance of the Werfen communities with respect to the recovery and provide a comparison with recently published data from other palaeogeographic regions.

Palaeoecology and recovery throughout the Werfen Formation.

The analysis and reconstruction of palaeoecological and environmental conditions during the aftermath of the end-Permian mass extinction is not straight forward. Schubert and Bottjer (1995) were among the first who suggested that the Early Triassic was a time interval during which benthic ecosystems were characterised by a distinctive ecology involving reduced competition (Hofmann *et al.* 2013b) or low ecospace utilization (Buatois and Mángano 2011) when compared to background times that are characterised by a well diversified and highly structured biosphere. Accordingly, many traits that are typically observed in benthic ecosystems such as low diversity, wide environmental range, or dominance of "disaster" taxa may reflect intrinsic controls as a result of the diversity loss and ecospace vacation. Other workers (e.g. Twitchett and Wignall 1996) argued that the poverty seen in Early Triassic ecosystems reflects extrinsic controls such as ongoing environmental stress. However, this view ignores the impact of the extinction on ecosystems itself. Furthermore, data that were perceived as independent evidence for environmental stress (i.e. lamination, abundant pyrite, isotopic signals) may be directly linked to ecosystem function such as biogenic sediment mixing (Erwin 1993; Canfield and Farquhar 2009; Hofmann *et al.* 2011). Hofmann *et al.* (2013a) suggested that simple and low-diverse ecosystems, especially of the earliest Triassic, reflect the consequences of the extinction in the first place. This does not necessarily mean that environmental stress did not play a role but the apparent relationship between fundamental loss of biodiversity and simple ecosystems clearly diminishes the usability of palaeoecological and ichnological models to reconstruct environmental conditions. Possibly a great number of Early Triassic communities and ichnofaunas would be, and in fact were (Twitchett and Wignall 1996), interpreted as highly stressed without consideration of the effects of extinction.

The early aftermath of the extinction (Mazzin Member). –The bulk richness of the communities is 9 and 11 respectively, which appears not particularly low even when compared to more advanced communities of the later Early Triassic presented in this study and published elsewhere (see Hofmann *et al.* 2013c). This appears to be related to a short term survival of Permian taxa (e.g. bellerophondid Gastropods, and the bivalve *Towapteria*) besides an already typical Early Triassic fauna including the genera *Claraia, Unionites, Eumorphotis, Neoschizodus, Pteria,* or *Coelostylina* (Fig. 20). The Permian elements disappeared during deposition of the Mazzin Member making them local cases of the dead clade walking phenomenon (see Kaim and Nützel 2011 for discussion). Given the proximity to the mass extinction, there is no conclusive evidence for environmental stress in the basal part of the Mazzin Member.The interval of maximum poverty is recorded in the mid-part of the Member, where a number of samples are clearly dominated by *Claraia aurita.* This signal could in fact represent a transient resurgence of environmental stress. This is supported by the observation that the general sedimentary facies does not change in the Mazzin Member, which could otherwise provide an alternative explanation for the faunal pattern. The *Neoschizodus orbicularis* association, which is observed in the upper part of the Member, records again relatively low dominance values and comparably high diversities. In sum, the Mazzin Member possibly indicates some phases of environmental stress but the overall richness and ecological structure is not fundamentally different from other Griesbachian communities. In addition, it is noted that individual samples which show close affinities

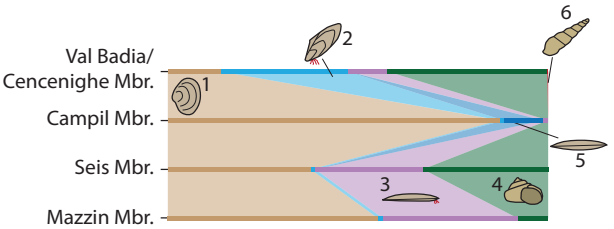

Fig. 19. Ecological guilds (after Aberhan 1994) througout sampled members of Werfen Formation (1-shallow infaunal suspension feeder, 2-semi-infaunal suspension feeder, 3-attached epifaunal suspension feeder, 4-epifaunal grazer, 5-free-lying epifaunal suspension feeder, 6-epifaunal carnivore).

in terms of dominant taxa can be quite heterogeneous with respect to accessory taxa. This suggests that the low sample diversity could be driven by sampling effects, which would argue for higher original local diversities.

A decline during the Dienerian (Seis/Siusi Member). – In general, richness, dominance values as well as bulk richness are not significantly different in the Seis Member when compared to the Mazzin Member. As noted above, the different clusters of the Seis/Siusi data set reflect a stratigraphic signal and a high variability of few dominating species. Apart from the short interval dominated by *Claraia clarai* at the base of the Member, general species composition does not change notably over time. The ecological structure is also rather uniform throughout the member. As already noted, sample richness decreases and dominance values increase towards the top of the Member which points to deterioration in environmental conditions. This is in accordance with the observation that in the upper part of the Seis/Siusi Member, sedimentary facies shifts from an open marine, mainly calcareous depositional system, to more restricted marine environment with high input of fine-grained siliclastic material, which certainly has had an effect on the benthic fauna (i.e. salintiy stress; Nützel and Schulbert 2005). Accordingly, the interregional significance of this signal is uncertain.

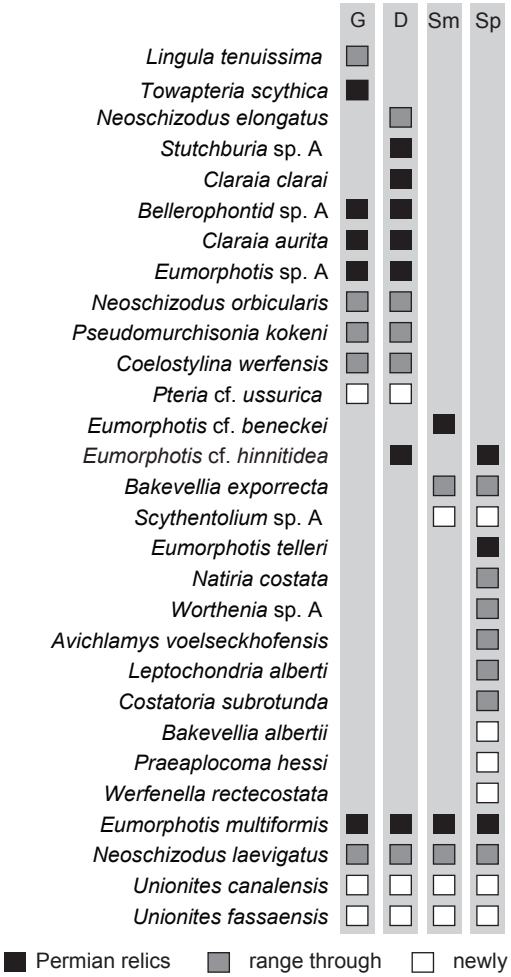

Fig. 20. Stratigraphic ranges of observed macrofossils throughout the Werfen Formation. G-Griesbachian, D-Dienerian, Sm-Smithian, Sp-Spathian.

An overall compilation of the diversity that involves not only the sample richness, but mean standing diversity, as well as origination and extinction rates shows comparable trends in both sections studied (Fig. 21A, B). A composite curve for the whole Werfen Formation (Fig. 21C) demonstrates that this is a real pattern because the taxa did not only disappear during the Dienerian but actually did not return later, too. The same pattern is observed in the general range of taxa (Fig. 20). The Dienerian-Smithian transition, thus, records the most notable disappearance of invertebrate taxa (i.e. *Pseudomurchisonia kokeni, Coelostylina werfensis, Bellerophontid* sp. A *,Neoschizodus orbicularis ,Pteria* cf. *ussurica , Claraia aurita ,Eumorphotis* sp. A *,Stutchburia* sp. A *Neoschizodus elongatus, Claraia clarai*) in the whole Formation. Accordingly, even if local environmental deterioration might have played a role, the upper Dienerian can be portrait as a crises interval for benthic ecosystems, at least in this palaeogeographic region. If stress would have been local, it can be assumed that taxa would have re-established later. Further support for this hypothesis is provided by observation from the Gastropod Oolite Member. Although these strata are very similar to the lower Seis Member in terms of sedimentary environment, it contains almost no benthic fauna and bioturbation is virtually absent. This could indicate that ecosystems experienced a set back before or during the deposition of these strata.

The Smithian (Gastropod Oolite- and Campil Member). – These Members record the lowest richness- and the highest average dominance values of the whole Formation. The sedimentary facies of the Campil Member is characterised by a high input of siliclastic material, which was possibly accompanied by fluctuations in salinity. Variable salinities would impede existence of stenohaline organisms. However, other aspects that might have had an influence on this low diverse signal must be considered. The strata of the Campil Member are almost exclusively composed of siliclastic material, which hampers preservation of calcitic shell material due to early diagenetic dissolution. If fossils are persevered, they are mostly present as internal moulds in sandstone, which reduces the possibility of species identification. Fine-grained intervals are very rarely well exposed, which would introduce yet another bias towards a low-diversity signal.

The recovery status recorded by Smithian strata thus remains unclear. However, some observations and published data could indicate that recovery of benthic ecosystems modestly advanced during the Smithian. The scarce record of previously not observed bivalve taxa (e.g. *Scythentolium* and *Costatoria*) and the first post-extinction appearance of the ophiuroid resting trace *Asteriacites* imply that restoration somewhat proceeded. Furthermore, Broglio Loriga *et al.* (1990) documented the establishment of several new bivalve taxa in the upper

Campil Member, which is also observed the Smithian succession of Hungary. This suggests that potential recovery may be in fact masked by this 'terrigenous event' (Broglio Loriga *et al.* 1990) in the Werfen Formation.

The end-Smithian and the Smithian/Spathian transition are not well documented in the Werfen Formation. For the reasons outlined above and the fact that the uppermost Campil Member and some parts of the lower Val Badia Member record supratidal conditions, a reliable reconstruction of recovery is not possible. The range of taxa considered herein (Fig. 20) shows no extinction among benthic clades across this interval. This suggests that this transition, which is pivotal for the general recovery (see discussion below), had no marked effect on benthic ecosystems.

The Spathian (Val Badia- and Cencenighe Member). – For the most part, ecological structure, diversities and dominance values of these two units do not differ from those recorded in the lower part of the Werfen Formation. Only in some levels of the upper Val Badia- and some levels in the Cencenighe Member, sample richness may be somewhat higher and dominance values are notably smaller in comparison to older communities. However, sample densities and specimen number is significantly lower than in the Mazzin- and the Seis/Siusi Members. The rarefaction curve of the most diverse association (*Bakevellia exporrecta* association) indicates a much higher expected diversity. Both aspects suggest that the signal obtained from the Spathian suffers from under-sampling. Accordingly, the rather modest relaxation seen in the Spathian communities would be more pronounced if standardised sampling would have been possible. Additionally, a much more balanced guild structure and somewhat higher guild diversity (Fig. 17), and a significant increase of newly evolved taxa (Figs. 20, 21C) indicates that the Spathian records the most advanced recovery stage of the Werfen Formation. The paucity or rather the general lack of abundant benthic fauna in the Cencenighe Member most likely reflects the dominance of marginal marine and intertidal facies in this Member. The same is true for the overlying San Lucano Member, in which the fossil record is too poor for taking quantitative samples.

An update for the recovery dynamics of the Werfen Formation

The herein presented data provides evidence for a modest recovery throughout the lower part of the Werfen Formation. Overall diversity is gradually increasing towards the Griesbachian-Dienerian transition (Fig. 21) with comparably high sample and association diversities recorded in the studied sections. The Dienerian documents a decline of benthic ecosystems and the Dienerian-Smithian transition represents the most notable caesura for benthic ecosystems (Figs. 20, 21). The Smithian record is biased because of local environmental conditions and a sedimentary facies which is detrimental for the preservation of calcareous fossils. Despite of the low sampling density, the Spathian probably records the most advanced faunas.

The macrofauna data contribute to the recovery trajectory presented by Twitchett and Wignall (1996), which was based on ichnological data. In contrast to that study, we see no evidence for anoxic conditions, which were proposed to have been widespread during the Griesbachian (see also Wignall and Twitchett 1996). The trophic structure of the fauna including infaunal and epifaunal suspension feeders as well as epifaunal grazers argues against long-lasting oxygen-depletion in the ocean water (Wignall 1993). We consider it much more likely that the evidence for anoxia in the lower Werfen Formation (sediment lamination, abundant pyrite, low bioturbation; Twitchett and Wignall 1996) expresses simply the

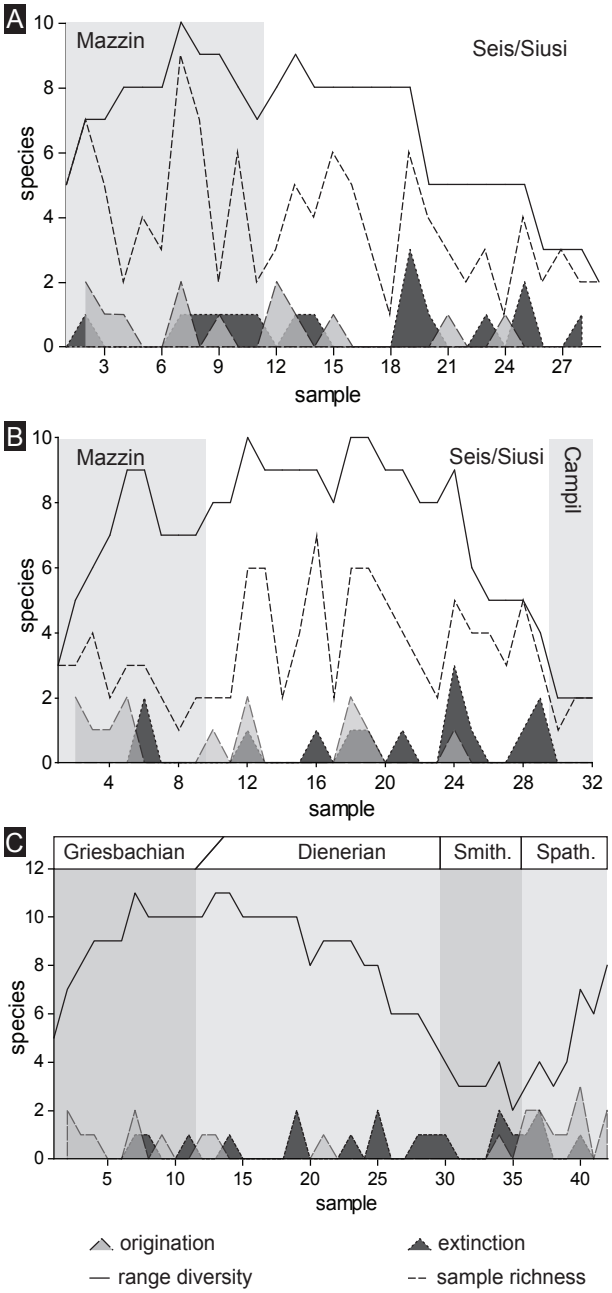

Fig. 21. Diversities and sample richness throughout the lower Werfen Formation at the Aferer Geisler (A), and the Rosengarten/Catinaccio (B) localities. C, Synthetic diversity curves throughout the whole Werfen Formation

extinction of burrowers (see also Erwin 1993; Hofmann *et al.* 2011) and not an exclusion of infauna by unfavourable environmental conditions. As discussed by Hofmann *et al.* (2013a), the paucity of Griesbachian faunas possibly reflects first of all the impact of the extinction. This is also supported by the observation that Mazzin communities do not significantly differ in terms of ecological structure and diversity. If anoxic conditions would prevail during much of the Griesbachian, a more profound recovery signal is expected with increasing stratigraphic distance from the extinction horizon. However, the opposite is the case: The evidence presented herein suggests that the recovery was impeded by environmental decline in the course of the Dienerian. Concerning the remaining substages of the Early Triassic, our data largely confirm the statements made by Twitchett and Wignall (1996).

Comparison with other localities

In a series of recent studies (Hautmann *et al.* 2013, Hofmann *et al.* 2013a, b, c), we provided an updated picture on the Early Triassic recovery at the eastern tropical Panthalassa margin from strata of the Western U.S. Because this succession records a stratigraphically well calibrated (Brayard *et al.* 2013; Hofmann *et al.* 2013c) and probably the most continuous and succession of benthic ecosystems throughout the Early Triassic, a comparison with the Werfen signal is aimed to extract general recovery trends and to distinguish local from interregional signals.

In the western U.S., the early post-extinction interval is characterised by low diverse communities. Towards the upper Griesbachian, shallow marine settings may exhibit locally higher diversities with up to 12 species recorded per association (Hofmann *et al.* 2013a). Strata of the Werfen Formation contain communities with a comparable bulk richness of 11 species. The upper Dinwoody Formation (?middle to late Dienerian) records a decline back to low-diverse communities (Hofmann *et al.* 2013a). As the same pattern is observed in the Werfen Formation, we infer that Griesbachian-Dienerian recovery dynamics are similar in the palaeotropics. Although a similar palaeoecological study from other palaeogeographic regions are lacking, hitherto published data fit this pattern quite well. Shigeta *et al.* (2009) presented data from Far East Russia that show highest diversities for Griesbachian-Dienerian transition. Other reports of unexpectedly diverse faunas (Krystyn *et al.* 2003; Hautmann *et al.* 2011) that were hitherto referred to as refuge-communities (e.g. Twitchett *et al.* 2004) are Griesbachian in age. The Dienerian decline is also observed in Far East Russia by Shigeta *et al.* (2009). This pattern for the first two substages of the Early Triassic could be global and there are also hints for deleterious environmental conditions during the same time interval. There is evidence for anoxic conditions from the low to high latitude eastern Panthalassa margin (Ware *et al.* 2011; Grasby *et al.* 2012) as well as for the equatorial Tethys (Hermann *et al.* 2011).

The Smithian communities of the Western U.S. are significantly more diverse, especially in mid- and inner shelf environments of the Sinbad Formation (Hofmann *et al.* in press). This difference is readily explained by the locally high siliclastic input seen in the Werfen Formation and closely related palaeogeographic regions (i.e. Hungary, Broglio Loriga *et al.* 1990). The end-Smithian and Smithian-Spathian transition, which represents the most critical Early Triassic time interval for ammonoids, was a non-event for benthic ecosystems in the Western U.S. and Northern Italy. The most advanced recovery stages in both regions are observed in Spathian strata (Hofmann *et al.* 2013b, c). However, this recovery signal is less pronounced in the Werfen Formation. This could result from local facies conditions and a significantly lower sampling density. A considerable difference though is the virtual absence of some benthic clades such as articulated brachiopods, crinoids and echinoids in the Werfen Formation when compared to the western U.S. (see Hofmann *et al.* 2013b). This could be interpreted as a more protracted restoration in the western margin of the tropical Tethys. Together with the sparse record of ammonoids in the upper Werfen Formation, this could point to a generally unfavourable facies for strongly stenohaline organisms. Another possibility is that the western end of the tropical Tethys received little exchange with open oceanic currents which would have impeded the immigration of taxa with planktonic larval stages.

Conclusions

The quantitative palaeoecological analysis enabled a comprehensive reconstruction of benthic ecosystems throughout the Lower Triassic Werfen Formation. The succession of faunas and accompanying palaeoecological parameters suggests that benthic ecosystems experienced modest recovery during the Griesbachian and early Dienerian. The comparison of the Mazzin and the Seis/Siusi Member indicates a certain decline in environmental conditions in the course of the Dienerian, rather than the expected progress in recovery with increasing stratigraphic distance from the mass extinction event. This pattern suggest that the deleterious environmental conditions which were proposed to have been present throughout the Griesbachian had either little effect on the benthos or were not as persistent as assumed. The Smithian diversity-low in the Werfen Formation was caused by an episode of high influx of siliclastic material, which had a local detrimental effect on ecosystems. The Spathian marks a second recovery pulse. A comparison with hitherto published recovery dynamics from other regions suggests that the Griesbachian recovery signal was an interregional pulse that has been set back during Dienerian times. The Smithian signal of the Werfen Formation is strongly biased due to local facies effects and other regions (most notably the western U.S.) show modest recovery during this substage. The Spathian marks the definite onset of ecological recovery but the western

margin of the tropical Tethys lagged behind the tropical margin of the eastern Panthalassa Ocean probably due to local facies effects and a somewhat restricted exchange with open oceanic circulation.

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References

Aberhan, M. 1992: Palökologie und zeitliche Verbreitung benthischer Faunengemeinschaften im Unterjura von Chile. Beringeria, 5, 1-174.

Aberhan, M. 1994: Guild-structure and evolution of Mesozoic benthic shelf communities. Palaios, 9, 516-545.

Blakey, R. 2012: Global Paleogeography. http://www2.nau.edu/rcb7/globaltext2.html (accessed May 2012).

Brayard, A., Bylund, K. G., Jenks, J. F., Stephen, D. A., Olivier, N., Escarguel, G.,Fara, E., & E. Vennin 2013: Smithian ammonoid faunas from Utah: implications for Early Triassic biostratigraphy, correlation and basinal paleogeography. Swiss Journal of Palaeontology. Volume 132, 141-219.

Broglio Loriga, C., D. Masetti & C. Neri 1982: La Formazione di Werfen (Scitico) delle Dolomiti occidentali. Rivista Italiana di Paleontologia e Stratigrafia, 88, 501-598.

Broglio Loriga, C., F. Góczán, J. Haas, K. Lenner, C. Neri, A. Oravecz-Scheffer, R. Posenato, I. Szabó & Á. Tóth-Makk 1990: The Lower Triassic sequences of the Dolomites (Italy) and Transdanubian Mid-Mountains (Hungary) and their correlation. Mem. Sci. Geol., 42, 41-103.

Buatois, L. A. & M. G. Mángano 2011: The déjà vu effect: Recurrent patterns in exploitation of ecospace, establishment of the mixed layer, and distribution of matgrounds. Geology, 39, 1163-1166.

Canfield, D. E. & J. Farquhar 2009: Animal evolution, bioturbation, and the sulfate concentration of the oceans. Proceedings of the National Academy of Sciences of the United States of America, 106, 8123-8127.

Erwin, D. H. 1993: The Great Paleuzoic Crisis: Life and Death in the Permian. Critical
Moments in Paleobiology and Earth History Series. Columbia University Press, New
York. 327 pp.

Grasby, S. E., B. Beauchamp, A. Embry & H. Sanei 2013: Recurrent Early Triassic ocean anoxia. Geology, 41, 175-178.

Hallam, A. 1991: Why was there a delayed radiation after the end-Paleozoic extinctions? Historical Biology, 5, 257-262.

Hammer, Ø., Harper, D. A. T. and P. D. Ryan 2001. Past: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica, 4,

Hautmann, M., H. Bucher, T. Brühwiler, N. Goudemand, A. Kaim & A. Nützel 2011: An unusually diverse mollusc fauna from the earliest Triassic of South China and its implications for benthic recovery after the end-Permian biotic crisis. Geobios, 44, 71-85.

Hautmann, M., A. B. Smith, A. J. McGowan & H. Bucher 2013: Bivalves from the Olenekian (Early Triassic) of south-western Utah: systematics and evolutionary significance. Journal of Systematic Palaeontology, 11, 263-293.

Hermann, E., P. A. Hochuli, S. Méhay, H. Bucher, T. Brühwiler, D. Ware, M. Hautmann, G. Roohi, K. ur-Rehman & A. Yaseen 2011: Organic matter and palaeoenvironmental signals during the Early Triassic biotic recovery: The Salt Range and Surghar Range records. Sedimentary Geology, 234, 19-41.

Hofmann, R., N. Goudemand, M. Wasmer, H. Bucher & M. Hautmann 2011: New trace fossil evidence for an early recovery signal in the aftermath of the end-Permian mass extinction. Palaeogeography, Palaeoclimatology, Palaeoecology, 310, 216-226.

Hofmann, R., Hautmann, M., & H. Bucher 2013a: A new paleoecological look at the Dinwoody Formation (Lower Triassic, western U.S.): intrinsic versus extrinsic controls on ecosystem recovery after the end-Permian mass extinction. Journal of Paleontology, 87, 854-880.

Hofmann, R., M. Hautmann, M. Wasmer & H. Bucher 2013b: Palaeoecology of the Spathian Virgin Formation (Utah, USA) and Its Implications for the Early Triassic Recovery. Acta Palaeontologica Polonica, 58, 149-173.

Hofmann, R., Hautmann, M., Brayard, A., Nützel, A., Bylund, K.G., Jenks, J., Vennin, E., Olivier, N., & H. Bucher 2013c: Recovery of benthic marine communities from the end-Permian mass extinction at the low-latitudes of Eastern Panthalassa. Palaeontology.
Kaim, A. & A. Nützel 2011: Dead bellerophontids walking - The short Mesozoic history of the Bellerophontoidea (Gastropoda). Palaeogeography Palaeoclimatology Palaeoecology, 308, 190-199.

Krystyn, L., S. Richoz, A. Baud & R. J. Twitchett 2003: A unique Permian-Triassic boundary section from the Neotethyan Hawasina Basin, Central Oman Mountains. Palaeogeography, Palaeoclimatology, Palaeoecology, 191, 329-344.

Metcalfe, B., R. J. Twitchett & N. Price-Lloyd 2011: Changes in size and growth rate of 'Lilliput' animals in the earliest Triassic. Palaeogeography Palaeoclimatology Palaeoecology, 308, 171-180.

Morisita, M. 1959: Measuring of interspecific association and similarity between communities. Mem. Fac. Sci. Kyushu Univ. Ser. E (Biol.), 3, 65-80.

Neri, C. & R. Posenato 1985: New biostratigraphical data on uppermost Werfen formation of western Dolomites (Trento, Italy). Geologisch-Paläontologische Mitteilungen Innsbruck, 14, 83-107.

Neyman, A. A. 1967: Limits to the application of the trophic group concept in benthic studies. Oceanology, 7, 149-155.

Noé, S. & W. Buggisch 1994: Sequence stratigraphy in Late Permian and Lowest Triassic of the Southern Alps (Dolomites; northern Italy) with special regard to the Permian/Triassic boundary. Jahrbuch der Geologischen Bundesanstalt, 137, 297-318.

Nützel, A. 2005: A new Early Triassic gastropod genus and the recovery of gastropods from the Permian/Triassic extinction. Acta Palaeontologica Polonica, 50, 19–24.

Nützel, A. & C. Schulbert 2005: Facies of two important Early Triassic gastropod lagerstätten: implications for diversity patterns in the aftermath of the end-Permian mass extinction. Facies, 51, 480-500.

Perri, M.C. 1991: Conodont biostratigraphy of the Werfen Formation (Lower Triassic), Southern Alps, Italy. Bolletino della Societa Paleontologia Italiana, 30, 23-46.

Posenato, R. 2008: Global correlations of mid Early Triassic events: the Induan/
Olenekian boundary in the Dolomites (Italy). Earth Sci. Rev. 91, 93-105.

Posenato, R. 2009: Survival patterns of macrobenthic marine assemblages during the end-Permian mass extinction in the western Tethys (Dolomites, Italy). Palaeogeography Palaeoclimatology Palaeoecology, 280, 150-167.

Schubert, J. K. & D. J. Bottjer 1995: Aftermath of the Permian-Triassic mass extinction event: Paleoecology of Lower Triassic carbonates in the western USA. Palaeogeography, Palaeoclimatology, Palaeoecology, 116, 1-39.

Shigeta, Y., Zakaharov, Y. D., Maeda, H., & A. M. Popov, A. M. (eds.) 2009: The Lower Triassic system in the Abrek Bay area, South Primorye, Russia. National Museum of Nature and Science Monographs 38, Tokyo.

Twitchett, R. J. & P. B. Wignall 1996: Trace fossils and the aftermath of the Permo-Triassic mass extinction: Evidence from northern Italy. Palaeogeography, Palaeoclimatology, Palaeoecology, 124, 137-151.

Twitchett, R. J., L. Krystyn, A. Baud, J. R. Wheeley & S. Richoz 2004: Rapid marine recovery after the end-Permian mass-extinction event in the absence of marine anoxia. Geology, 32, 805-808.

Ware, D., J. F. Jenks, M. Hautmann & H. Bucher 2011: Dienerian (Early Triassic) ammonoids from the Candelaria Hills (Nevada, USA) and their significance for palaeobiogeography and palaeoceanography. Swiss Journal of Geosciences, 104, 161-181.

Wignall, P. B. 1993: Distinguishing between Oxygen and Substrate Control in Fossil Benthic Assemblages. Journal of the Geological Society, 150, 193-196.

Wignall, P. B. & A. Hallam 1992: Anoxia as a cause of the Permian/ Triassic mass extinction: facies evidence from northern Italy and the western United States. Palaeogeography, Palaeoclimatology, Palaeoecology, 93, 21-46.

Wignall, P. B. & R. J. Twitchett 1996: Oceanic anoxia and the end permian mass extinction. Science, 272, 1155-1158.

Wignall, P. B., Kozur, H. & A. Hallam 1996: On the timing of palaeoenvironmental changes at the Permo-Triassic (P/TR) boundary using conodont biostratigraphy, Historical Biology: An International Journal of Paleobiology, 12, 39-62.

Conclusions and Outlook

Key results

This thesis adds crucial aspects to the understanding of the recovery from the end-Permian mass extinction. It has been shown in the **chapters 1**, **3**, and **5** that benthic ecosystems experienced early recovery. Together with other recently published reports on comparatively diverse faunas from the Griesbachian time intervals (e.g. Shigeta et al., 2009; Hautmann et al., 2011), so-called refuges (see Twitchett et al., 2004) during the early extinction aftermath seem to have been rather the rule than the exception. The data presented herein suggest that diverse faunas were also present at low-latitudes, which were traditionally suggested to record persisting hostile conditions (i.e. shallow marine anoxia, Wignall and Hallam, 1992; Wignall and Twitchett, 1996). Furthermore, the data from the Dinwoody Formation (**chapter 3**) and the lower Werfen Formation (**chapter 5**) suggest that the early recovery signal was subsequently reset by new phases of interregional if not global environmental perturbations in the course of the Dienerian. If correct, this crisis interval would explain at least partially the long restoration. A second significant recovery signal is observed in the early Spathian of the Virgin Formation of the western U.S., which is of interregional significance (**chapter 2**). These ecosystems are more similar to Anisian (Middle Triassic) communities in terms of ecological structure, diversity as well as taxonomic composition. This suggests that the Spathian marks the global establishment of advanced recovery faunas and that Spathian communities represent the general root stock for typical Mesozoic ecosystems.

The diversity-partitioning-based recovery model proposed in **chapter 2** highlights the importance of beta-diversity to (i) reveal recovery stages and to (ii) detect 'non-actualistic' conditions of low competition among benthic invertebrate communities as a result of the extinction. A conclusive test of this model is presented in **chapter 4** and confirms the predictions made in **chapter 2**: a rising (community-) alpha diversity and more or less constant beta-diversity throughout the studied time interval. This suggests that the Early Triassic was a period with low ecosystem differentiation. Linked to this finding is the hypothesis that benthic ecosystems experienced little competition and that species exploited a wide range of their ecological spectrum. What is referred to as "ecosystem saturation" in **chapter 2**, apparently did not occur in the investigated localities and time intervals. These studies revisit and support earlier suggestions (e.g. Schubert and Bottjer, 1995) that the Early Triassic benthic recovery was mainly driven by intrinsic aspects. For instance the high portion of eurytopic taxa is readily explained by low diffuse competition in Early Triassic ecosystem (see **chapter 2**) and the low diversity in the immediate aftermath (see **chapter 3** and **5**) of the extinction simply reflect the dramatic loss in biodiversity and not necessarily environmental stress.

The most detailed diversity curves have been obtained from studies on the nekton. Ammonoids and conodonts, which are at least secondary consumers, have high evolutionary rates and thus are sensitive for reflecting effects of environmental perturbations on marine ecosystems. Previous analyses have shown that ammonoids (Brayard et al., 2009) and conodonts (Orchard, 2007) suffered most from an end-Smithian crisis that was probably caused by dramatic climatic changes during the Smithian substage (Romano et al., 2013). The analyses of coveal benthic ecosystems (**chapter 4**) suggests that, at least in the Western U.S., the end-Smithian was a non-event for level bottom faunas. The Smithian-Spathian boundary documents a change in dominant species but no extinction among benthic groups.

In summary, with respect to benthic ecosystems the studies carried out for this thesis provide evidence for (i) an interregional recovery signal around the Griesbachian-Dienerian, (ii) a subsequent interregional setback during the ?late Dienerian, (iii) only little effects of the 'end-Smithian' crisis interval, and, finally, (iv) it is put forward that typical Early Triassic phenomena such as low diversity and wide environmental range of benthic invertebrate taxa reflect intrinsic controls caused by the dramatic biodiversity loss and ecospace vacation as a direct result of the mass extinction.

Directions for future research

Nekton vs. benthos recovery. One puzzling aspect of the Early Triassic recovery is that nektonic and benthic clades show a notably different restoration pattern. (Table 1). To integrate these results will be of utmost importance to understand the recovery in general. The open water column and the ocean bottom are two principle domains of the marine ecosystem with different physical and chemical constraints as well as ecological structures. The varying behaviour could simply result from the fact that pelagic free-swimming clades are typically predators, or at least secondary consumers, which are much more sensitive to ecological changes and prone to extinction. Benthic ecosystems apparently show a notable decline in the course of the Dienerian (**chapter 3, 4,** and **5**), which seems to be the case for nektonic groups as well (personal communication, D. Ware, Zürich). In contrast, the biggest nekton-crises at the end of the Smithian had very little effect on benthic ecosystems (**chapter 4**). This suggests that underlying processes and/or the environmental triggers were different in both time intervals. If further substantiated, this pattern will help to elucidate the nature and causes of environmental changes throughout the Early Triassic.

Beta-diversity, ecosystem differentiation, and diversification. The diversity partitioning-based model introduced in **chapter 2** potentially explains why the radiation of benthic groups started considerably after definite onset of recovery. It is proposed that elevated competition, after

Table 1. Recovery during important time intervals of the Early Triassic of ammonoids and benthic clades. Ammonoids mainly after Brayard et al. (2006, 2009), Ware D., personal communication. Benthos data as presented in this thesis.

time interval	nekton (ammonoids)	benthos (mainly bivalves, gastropods)
Griesbachian	gradual and modest recovery	
Dienerian	radiation and extinction	decline
Dienerian-Smithian boundary	modest radiation	unknown, possible crisis
Smithian	recovery, explosive radiation	modest recovery
Smithian-Spathian boundary	extinction	no extinction
Spathian	recovery, explosive radiation	recovery, ?beginning radiation

community alpha diversity exceeded a certain threshold value (which is not determined, yet), could force species into their ecological optima, and thus would cause an ecosystem differentiation along environmental gradients. An important effect of this would be that beforehand wide ranging species would split into increasingly specialised species over time. This would result in locally elevated beta-diversities which contribute to a general rise in overall biodiversity (gamma-diversity) of the faunal province and also on a global scale. This could be an underlying intrinsic process of the Middle Triassic radiation of bivalves (e.g. Posenato, 2008). An ultimate test for the validity of this model and the plausibility of this process could be provided by a comparison with pre-extinction ecosystems and younger post-extinction ecosystems that straddle this diversification interval.

To test the validity of this model, the following predictions should be confirmed: (i) intrabasinal beta-diversities of adjacent communities over a range of subhabitats of pre-extinction ecosystems should be higher when compared to the Early Triassic, (ii) beta-diversities should gradually increase during the late Early Triassic and throughout the Middle Triassic, and (iii) community alpha diversity should level off some time after the "ecosystem saturation".

References

Brayard, A., Bucher, H., Escarguel, G., Fluteau, F., Bourquin, S., and Galfetti, T., 2006. The Early Triassic ammonoid recovery: Paleoclimatic significance of diversity gradients. Palaeogeography Palaeoclimatology Palaeoecology, 239: 374-395.

Brayard, A. et al., 2009. Good Genes and Good Luck: Ammonoid Diversity and the End-Permian Mass Extinction. Science, 325(5944): 1118-1121.

Hautmann, M., Bucher, H., Brühwiler, T., Goudemand, N., Kaim, A., and Nützel, A. 2011. An unusually diverse mollusk fauna from the earliest Triassic of South China and its implications for benthic recovery after the end-Permian biotic crisis. Geobios 44(1): 71-85.

Orchard, M.J., 2007. Conodont diversity and evolution through the latest Permian and Early Triassic upheavals. Palaeogeography Palaeoclimatology Palaeoecology, 252(1-2): 93-117.

Romano, C., Goudemand, N., Vennemann, T. W., Ware, D., Schneebeli-Hermann, E., Hochuli, P. A., Brühwiler, T., Brinkmann, W. and Bucher, H. 2013. Climatic and biotic upheavals following the end-Permian mass extinction. Nature Geoscience, 6: 57-60.

Schubert, J.K. and Bottjer, D.J., 1995. Aftermath of the Permian-Triassic Mass Extinction Event - Paleoecology of Lower Triassic Carbonates in the Western USA. Palaeogeography Palaeoclimatology Palaeoecology, 116(1-2): 1-39.

Shigeta, Y., Zakaharov, Y. D., Maeda, H., & A. M. Popov, A. M. (eds.) 2009: The Lower Triassic system in the Abrek Bay area, South Primorye, Russia. National Museum of Nature and Science Monographs 38, Tokyo.

Twitchett, R.J., Krystyn, L., Baud, A., Wheeley, J.R. and Richoz, S., 2004. Rapid marine recovery after the end-Permian mass-extinction event in the absence of marine anoxia. Geology, 32(9): 805-808.

Wignall, P.B. and Hallam, A., 1992. Anoxia as a Cause of the Permian Triassic Mass Extinction - Facies Evidence from Northern Italy and the Western United-States. Palaeogeography Palaeoclimatology Palaeoecology, 93(1-2): 21-46.

Wignall, P.B. and Twitchett, R.J., 1996. Oceanic anoxia and the end Permian mass extinction. Science, 272(5265): 1155-1158.

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As I enjoyed family life for a large part of my time as a PhD stundent, I was hardly involved in social activities of the PIM group. I would like to take this as an excellent opportunity to quote J.R.R. Tolkien's Bilbo Baggins: "I don't know half of you half as well as I should like; and I like less than half of you half as well as you deserve." So I thank everybody whose path I crossed during the last 4.5 years for their support, understanding and tolerance for my non-existing social commitment and bad jokes. Especially mentioned are: Christian Klug, Kenneth De Baets, Carlo Romano, Åsa Frisk, Elke Schneebeli-Hermann, Thomas Brühwiler, Jasmina Hugi, Carol Naglik, David Ware, Borhan Bagherpour, Linda Frey, Christian Kolb, Constanze Bickelmann, Morgane Brosse, Nico Goudemand, Claude Monnet, Max Meier, Anna Sanson, and Jorge Carillo.

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Appendix

I List of publications

Associated articles

Hofmann, R., Buatois, L. A. B., Mángano, M.G., and MacNaughton, R. B. (in prep): Devastation of the mixed layer in marine sediments as a result of the end-Permian mass extinction. *Submission planned for 02/2014*

Frisk, A. M., **Hofmann, R.**, Hautmann, M., and Bucher, H. (in prep): Early Triassic Microbialite faunas of western China. *Submission planned for 02/2014*

Hofmann, R., Hautmann, M., and Bucher, H. (in prep): Benthic recovery in the Werfen Formation. *Submission planned for 02-03/2014*. (***chapter 5***)

Hofmann, R., Hautmann, M., Brayard, A., Nützel, A., Bylund, K.G., Jenks, J., Vennin, E., Olivier, N. and Bucher, H. (2013): Recovery of benthic marine communities from the end-Permian mass extinction at the low-latitudes of Eastern Panthalassa. *Palaeontology*. (***chapter 4***)

Hofmann, R., Hautmann, M., and Bucher, H. (2013): A new paleoecological look at the Dinwoody Formation (Lower Triassic, western U.S.): intrinsic versus extrinsic controls on ecosystem recovery after the end-Permian mass extinction. *Journal of Paleontology.* 87(5), 854–880. doi: 10.1666/12-153. (***chapter 3***)

Hofmann, R., Hautmann, M., Wasmer, M. and Bucher H. (2013): Palaeoecology of the Virgin Formation (Utah, USA) and its implications for the Early Triassic recovery. *Acta Palaeontologica Polonica.* 58(1), 149–173, doi: 10.4202/app.2011.0060. (***chapter 2***)

Brayard, A., Vennin, E., Olivier, N., Escarguel, G., Bylund, K.G., Jenks, J., Stephen, D.A., **Hofmann, R.**, Goudemand, N. and Bucher, H (2011): Transient metazoan reefs in the aftermath of the end-Permian mass extinction. *Nature Geoscience.* 4(10), 693–697, doi:10.1038/ngeo1264.

Hofmann, R., Goudemand, N., Wasmer, M., Bucher, H. and Hautmann, M. (2011): New trace fossil evidence for an early recovery signal in the aftermath of the end-Permian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology.* 310(3-4), 216–226, doi:10.1016/j.palaeo.2011.07.014. (***chapter 1***)

Abstracts (attached hereafter)

Hofmann, R., Hautmann, M., Bucher, H. (2012): "…and they all lived happily ever after": Palaeoecology of benthic faunas in the aftermath of the end-Permian mass extinction. *Annual meeting of the "Paläontologische Gesellschaft". Terra Nostra* 2012/3, p. 81.

Hofmann, R., Hautmann, M., Bucher, H. (2012): No rules or just many exceptions? Spatial and temporal trends in benthic recovery from low-latitude settings. *IGCP 572 closing conference, Eger Hungary.*

Hofmann, R., Hautmann, M., Bucher H., Alistair J. McGowan, Andrew B. Smith (2011): Palaeoecology and taxonomic composition of the Spathian Virgin Limestone Fauna: implications for benthic recovery from the end-Permian mass extinction event. *Palass Meeting Plymouth.*

Hofmann, R., Hautmann, M., Bucher H. (2011): Ecological structure and taxa distribution in near shore habitats of the Virgin Formation (south-western Utah): Implications for the Early Triassic recovery. *9th Swiss Geoscience Meeting, Zürich, 2011.*

Hofmann, R., Hautmann, M., Goudemand, N., Wasmer, M. and Bucher, H., (2010): Dynamic recovery patterns of benthic ecosystems in the aftermath of the end-Permian mass extinction. *IPC 3, London 2010.*

Hofmann, R., Hautmann, M., Goudemand, N., Wasmer, M. and Bucher, H., (2010): Complex colonisation patterns of benthic communities in the immediate aftermath of the end-Permian mass extinction: New data from the Dolomites. In: Baud, A. and Bernecker, M. (eds): IGCP 572: Recovery of ecosystems after the Permian-Triassic mass extinction. *Field workshop at GUtech, Muscat, Oman February 20-26, 2010, abstract book.*

Hofmann, R. and Hautmann, M. (2009): Recovery of benthic marine communities after the end-Permian mass extinction: New data from the Werfen Formation (South Tyrol/Italy). *Annual Meeting of the "Paläontologische Gesellschaft". Terra Nostra* 2009/3: 52.

II Conference abstracts

Recovery of benthic marine communities after the end-Permian mass extinction: New data from the Werfen Formation (South Tyrol/ Italy)

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The Lower Triassic Werfen Formation (South Tyrol/ Italy) represents a key locality in the study of the Permian-Triassic mass extinction and, moreover, its aftermath. A so far unrecognised section at the slopes of the Aferer Geisler exposes a highly fossiliferous succession comprising strata from the uppermost Permian to the lower Olenekian. The Werfen Formation at the investigated locality is approximately 105 meters thick and includes the lithostratigraphic units Tesero Member, Mazzin Member, Andraz Horizon, Seis Member, Gastropod Oolith Member and possibly the lower part of the Campil Member. The depositional setting of the lower Werfen Formation is interpreted as a storm-dominated carbonate shelf environment characterised by laminated mudstones and tempestite-beds. Regressional phases are indicated by oolithic shoals and supratidal dolomites and claystones.

The initial post-extinction fauna of the lower Mazzin Member is dominated by shallow infaunal bivalves (*Unionites*, *Neoschizodus*), brachiopods (*Lingula*) and gastropods (*Coelostylina*). Rarely recorded are epifaunal bivalves (*Bakevellia*, *Eumorphotis* and *Towapteria*). In the upper Mazzin Member, the portion of epifaunal bivalves increases with the appearance and proliferation of the genus *Claraia*. Bioturbation is limited to a few burrows (*Planolites*) of vermiform deposit feeders. It is noted that the diversity is presumably higher than generally assumed for Griesbachian sections in the southern Alps. Although identification of species is problematic due to small adult size and preservation as internal molds, a multitude of morphotypes can be recognised. In particular small infaunal bivalves and gastropods thriving in the immediate aftermath of the extinction are prone to taxonomic lumping.

The fauna of the Seis and Gastropod Oolith Member is characterised by a notable increase of the average shell size and an increasing portion of epifaunal taxa. Brachiopods were not observed. Bioturbation is still sparse but burrows show significant higher diameter. New species appeared mainly among already established genera and individual assemblage-diversity remains low throughout the section.

A preliminary analysis of the field data suggests that the initial colonisation was rapid and involved opportunistic species organised in comparatively diverse early Triassic assemblages. Until the early Olenekian, however, the subsequent appearance of taxa did not result in higher habitat diversity. These observations confirm that the biotic recovery after the end-Permian mass extinction event was delayed for at least one million years, but they also show that the ecological structure during the lag phase was more complex than previously assumed. Future work on Early Triassic benthic communities from the USA, Greenland, and Pakistan will provide additional data that may help to better understand evolutionary dynamics in the wake of the greatest mass extinction event in Earth's history.

Complex colonisation patterns of benthic communities in the immediate aftermath of the end-Permian mass extinction: New data from the Dolomites

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The extensive exposures of the Lower Triassic Werfen Formation in South Tyrol (Italy) represent key localities in the study of the Early Triassic recovery interval. Fieldwork conducted in summer 2009 focused on a so far undocumented

section at the Aferer Geisler and on a section at the Rosengarten/Catinaccio. Both outcrops expose a continuous and particularly fossiliferous succession of the lower Werfen Formation. The Werfen Formation at the investigated localities amounts to 110 meters thickness and includes the following lithostratigraphic units: Tesero Member, Mazzin Member, Andraz Horizon, Seis Member, Gastropod Oolith Member, and the lower part of the Campil Member. The depositional setting of the lower Werfen Formation is interpreted as a storm-dominated carbonate shelf environment with occasional siliciclastic input. Predominating lithotypes are laminated mudstones and tempestite beds. Regressive phases are recorded by supratidal dolomites and siltstones.

The initial fauna of the lower Mazzin Member (Griesbachian) is dominated by shallow-infaunal bivalves (*Unionites*), infaunal brachiopods (*Lingula*), and epifaunal gastropods (*Coelostylina,* "*Bellerophon*"). Rarely recorded are epifaunal (*Eumorphotis* and *Towapteria*) and semi-infaunal bivalves (*Bakevellia*). In the upper Mazzin Member (Griesbachian), the portion of epifaunal bivalves increases with the appearance and proliferation of the genus *Claraia*. Bioturbation is limited to a few burrows (*Planolites*) of vermiform deposit feeders. The fauna of the Seis Member (Griesbachian-Dienerian) remarkably differs from that of the Mazzin Member in spite of a comparable facies. Several taxa have disappeared from the fossil record, and epifaunal forms (*Claraia* and *Eumorphotis*) are now dominating in most assemblages. The faunal shift coincides with a significant increase in average shell size. Moreover, a diverse infaunal ichnofauna with *Thalassinoides*, *Spongeliomorpha*, *Rhizocorallium,* and *Taenideum* has been observed for the first time from this early recovery stage in the Alps. However, overall diversity and the number of guilds in the body fossil record are slightly lower in the Seis Member than in the Mazzin Member. Towards the top of the section (lower Campil Member, Smithian), increased siliciclastic imput coincides with a notable drop in diversity, leading to paucispecific assemblages dominated by *Claraia* and *Unionites*.

From these observations, we infer that the factors that controlled the ecological structure during the early recovery phase were more complex than previously assumed. The comparatively high diversity in the early Griesbachian and the presence of a diverse ichnofauna in the late Griesbachian indicate that relatively advanced recovery stages were reached fairly early after the mass extinction event. However, the fact that body fossil assemblages and ichnofaunal associations significantly fluctuated within a comparatively short time interval suggests that environmental conditions were rapidly changing during the early recovery phase. Theses finds contradict the scenario of globally persisting shallow water anoxia that delayed biotic recovery for most of the Griesbachian. Rather than a sole mechanism that delayed biotic recovery globally, the new data indicate that the Griesbachian was a time of volatile environmental conditions that allowed at least local ecological ameliorations punctuated by smaller crises that repeatedly replaced faunal associations at various stages of recovery.

Dynamic recovery patterns of benthic ecosystems in the Aftermath of the end-Permian mass extinction

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The recovery of benthic ecosystems from the end-Permian mass extinction is generally assumed to have been severely protracted, not starting before the Spathian, approximately 2 m.a. after the crisis. However, the precise succession of fossil communities and their ecological significance has not been studied in detail so far. Bed by bed sampling at previously unstudied localities of the Werfen Formation (Alps, Italy) provided new insights into recovery patterns of benthic biota. Ecological parameters (guild diversity, species richness, dominance, etc.) suggest that the most advanced recovery stages in the investigated time interval (Pre-Spathian Early Triassic) were present during the middle and late Griesbachian. Robust ichnoassemblages in uppermost Griesbachian rocks reflect a significant recovery signal that has not been recognized before. The benthic diversity drastically declines towards the Dienerian/Smithian-boundary possibly as a result of local environmental stress. Our data show that the recovery does not reflect

a gradual increase of diversity and ecological complexity throughout the Early Triassic but out-of-phase fluctuations of numerous parameters. For instance, the increase of average body size among bivalves is not contemporaneous with diverse or ecological complex communities. Furthermore, the integration of our new trace fossil data with those from the literature shows that advanced recovery stages were reached quite early after the mass extinction on a global scale. The Early Triassic was possibly a time of volatile environmental conditions that allowed at least local ecological amelioration punctuated by smaller crises that repeatedly replaced faunal association at various stages of recovery.

Ecological structure and taxa distribution in near shore habitats of the Virgin Formation (south-western Utah): Implications for the Early Triassic recovery

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The recovery from the end-Permian biotic crisis is traditionally perceived to have been significantly delayed as a result of persistent deleterious environmental conditions and/or the extreme intensity of the extinction itself with an estimated species loss of 95% in the marine realm. Previous studies on the Virgin Formation of the Western U.S. put forward the view that harsh environmental conditions still persisted during the Spathian, at least 2 ma after the main extinction. However, palaeoecological analyses on the basis of species-level abundance data have hitherto not been carried out. Thus, very little is known on the actual ecological structure of the Virgin palaeocommunities and their spatial distribution.

We present a quantitative palaeoecological data-set, which is analysed with respect to the identified sedimentary environments. This integrated approach helps to discriminate between possible effects of the end-Permian mass extinction event and local environmental factors on alpha-diversity and ecological structure of the Virgin Fauna. Shallow subtidal environments yield the highest species richness and lowest dominance values as recorded in two benthic associations: the Eumorphotis ericius-association and the Protogusarella smithi-association, both of which contain 20 benthic species (bivalves, gastropods, brachiopods, echinoderms, and porifers). Tidal inlet deposits yield a low diverse fauna (Piarorhynchella triassica-association) with a very high dominance of filter feeders adapted to high energy conditions. Another comparably low diverse fauna is recorded by the Bakevellia exporrecta-association, which occurs in deposits of the offshore transition zone encompassing unconsolidated, mostly silicilastic substrates with a low preservation potential for calcareous body fossils. A single sample containing five bivalve species (Bakevellia costata-assemblage) is recorded from a marginal marine setting. The Virgin fauna yields a bulk diversity of 30 species (22 genera) of body fossils and 14 ichnogenera and, thus, represents the most diverse benthic fauna known so far from the Early Triassic.

Our results suggest that oceanographic conditions during the Early Spathian enabled ecosystems to rediversify without major abiotic limitations. However, taxonomical differentiation between habitats was still low, indicating a time lag between increasing within-habitat diversity (alpha-diversity) and the onset of taxonomical differentiation between habitats (beta-diversity). We suggest that taxonomical habitat differentiation after mass extinction events starts only after competition within habitats exceeded a certain threshold, which was not yet reached in the Spathian of the investigated area. This interpretation is an alternative to previous suggestions that the prevalence of generalistic taxa in the aftermath of mass extinction events reflects ongoing environmental stress. The onset of increasing beta diversity is a potential criterion for distinguishing two major recovery phases: the first ending with habitat saturation and the second ending with completion of ecosystem differentiation.

Palaeoecology and taxonomic composition of the Spathian Virgin Limestone Fauna: implications for benthic recovery from the end-Permian mass extinction event

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In a comprehensive study of benthic communities from the late Early Triassic Virgin limestone in Utah, USA, we identified 30 body fossil species and 14 ichnogenera. The Virgin limestone therefore contains the most diverse benthic fauna known from the Early Triassic, challenging previous claims that deleterious environmental conditions still persisted in this region during the Spathian. Analyses of quantitative species level data demonstrate that the ecological structure of subtidal palaeocommunities in the Virgin Limestone is not fundamentally different from that of Middle Triassic shallow-marine habitats. Simple communities are limited to locally stressed environments such as intertidal areas and lagoons, thus providing no indication of post-extinction effects. The high proportion of newly evolved taxa, mainly heteroconch bivalves, additionally suggests that recovery was well underway during the Early Spathian. However, taxonomical differentiation between habitats was still low, indicating a time lag between increasing within-habitat diversity (alpha-diversity) and the onset of taxonomical differentiation between habitats (beta-diversity). The onset of increasing beta-diversity may be useful to distinguish two major recovery phases: the first ending with habitat saturation and the second ending with completion of ecosystem differentiation.

No rules or just many exceptions? Spatial and temporal trends in benthic recovery from low-latitude settings

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Recent advances in the understanding of Early Triassic ecosystems suggest that the recovery from the end-Permian mass extinction was much more variable than traditionally suggested. By comparing low-latitude settings of the western Tethys (Werfen Formation of northern Italy) and eastern Panthalassa (Dinwoody Formation and Thaynes Group of the Western US) using quantitative palaeoecology, we aim to reconstruct ecosystem evolution in different palaeogeographical areas and to identify differences and general patterns in the recovery from the greatest mass extinction in Earth's history.

In the Werfen Formation, the immediate aftermath of the extinction records relatively diverse and balanced communities. In the course of the Griesbachian, simple, high-dominance communities predominate although some samples may show comparatively high diversities and low dominance values towards the upper Griesbachian. This trend culminates in the presence of moderately diverse and balanced faunas around the Griesbachian-Dienerian boundary interval and is mirrored in the ichnofaunas as well. In the course of the Dienerian, dominance, alpha diversity and community composition strongly fluctuates. In the lowermost Smithian interval, shelly fossils are virtually absent apart from some low-diverse shell pavements. Bioturbation is again significantly reduced. The remaining part of the Smithian is dominated by very low-diverse communities that strongly fluctuate in dominance values. The basal Spathian shows a remarkable increase in new species and the establishment of more balanced communities. Bioturbation becomes again abundant and the return of some "high recovery" ichnotaxa is observed. Alpha diversities rebound to the highest values recorded in the Werfen Formation.

In the Griesbachian and Dienerian rocks of the Dinwoody Formation of the western U.S., faunas locally exhibit relatively high alpha diversities and low dominance values. However, most samples of this time interval record rather highly-dominant, low-

diverse communities. During the Smithian (Thaynes Group and the Sinbad Formation), more balanced and slightly more diverse communities became established in outer and inner shelf settings with local occurrences of small, reef-like structures. The near shore habitats of the lower Spathian Virgin Formation record the most diverse and most balanced communities of the western U.S. of the Early Triassic.

It becomes apparent that the recovery patterns differed significantly between the two low-latitude settings. The western Tethys shows several pronounced ups and downs. A relaxation phase is observed at the base of the Griesbachian, which is related to the temporary presence of short-term survivors. A next strong recovery signal is observed around the Griesbachian/Dienerian-boundary. The communities of the same interval from Eastern Panthalassa indicate more stressed conditions except for some near-shore settings. In the western Tethys, a dramatic drop in benthic ecosystem complexity is recorded at the base of the Smithian. The subsequent "low" is likely related to high siliciclastic input, which was possibly accompanied by fluctuations in salinity. Smithian sections from Eastern Panthalassa do not show strong evidence for pronounced environmental stress and the ecological conditions improved with respect to the bulk Griesbachian and Dienerian record. The Spathian of the western Tethys marks a next notable restoration signal, which was, however, not fundamentally different to the first Griesbachian pulse in terms of alpha diversity and dominance of taxa. In eastern Panthalassa, this recovery signal is much more pronounced and the ecological and taxonomical recovery exceeds everything observed in earlier in the Triassic. In both palaeogeographic regions, the Early Spathian marks the establishment of many new taxa that add to the inherited diversity from the Smithian interval. With only little loss on the species and virtually no loss on the genus level, the Smithian-Spathian boundary was no caesura for benthic ecosystems.

In summary, restoration signals varied in their magnitude and stratigraphic position between both regions. To extract a general recovery pattern, additional data from other regions are necessary in order to factor out the local facies controls over the ecological structures of the benthic assemblages. It is furthermore noted that the well documented end-Smithian crisis of nektonic clades are not found in benthic ecosystems. By carefully integrating the variations in the recovery pattern among different clades and different regions, improved models on for environmental disturbances during the Early Triassic will be ultimately achieved.

"…and they all lived happily ever after": Palaeoecology of benthic faunas in the aftermath of the end-Permian mass extinction

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Key features of post extinction faunas are reduced ecological complexity, low diversity, and the dominance of taxa with broad environmental and geographic ranges. With respect to the aftermath of the end-Permian mass extinction, all these features have been reported in previous studies supporting the view that the delayed recovery after the end-Permian crisis largely resulted from persisting environmental stress. Among others, the fauna of the lower Triassic Virgin Formation (Early Spathian, Western U.S.) has repeatedly been cited as a typical example of a post extinction bottom fauna suffering from sustained environmental stress. However, this view is challenged by more recent studies that suggest that the recovery was a rather volatile process with notable restoration signals seen in various clades, palaeogeographic regions, and stratigraphic intervals.

Considering these advances, a reassessment of the ecology and diversity pattern of the Virgin fauna is of great importance for the understanding of biotic restoration and evolutionary processes after the biggest crises in the history of metazoan life. We integrated new quantitative fossil collections providing species level identifications and sedimentological data to discriminate between local facies effects and potential wide-ranging post extinction stress factors that influenced diversity and the ecological structure of benthic ecosystems.

The Virgin fauna yields a bulk diversity of 30 benthic species (22 genera) of body fossils and 14 ichnogenera and, thus, represents the most diverse marine assemblage reported from the Early Triassic so far. Benthic communities of open marine, shallow-subtidal environments are both, ecologically and taxononimcally, surprisingly diverse. Low

diverse communities are restricted to habitats providing evidence for local environmental stress unrelated to presumed post extinction effects. However, cluster analyses of the quantitative data set show that taxonomical differentiation between habitats was still low. This indicates a time lag between increasing within-habitat diversity (alpha diversity) and the onset of taxonomical differentiation between habitats (beta diversity). We suggest that taxonomical habitat differentiation after mass extinction events starts only when competition within habitats exceeded a certain threshold, which was not yet reached in the late Early Triassic of the investigated area.

This interpretation offers an alternative explanation to previous suggestions that the prevalence of generalistic taxa after the end-Permian mass extinction reflects persistent environmental stress. It also supports recent studies that emphasize that the recovery was well underway already during the Early Triassic. The onset of increasing beta diversity could be a potential criterion for distinguishing two major steps in recovery phases: the first ending with habitat saturation and the second ending with completion of ecosystem differentiation. Faunal successions that straddle recovery episodes could represent evolutionary test cases underlining the effect of ecosystem saturation, which possibly explains the sudden onset of taxonomic diversification during other phases of recovery and evolutionary radiations.

III Relevant co-authored publications

Transient metazoan reefs in the aftermath of the end-Permian mass extinction

by

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Transient metazoan reefs in the aftermath of the end-Permian mass extinction

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Recovery from the devastating Permian–Triassic mass extinction about 252 million years ago is usually assumed to have spanned the entire 5 million years of the Early Triassic epoch[1,2]. The post-crisis interval was characterized by large-scale fluctuations of the global carbon cycle and harsh marine conditions, including a combination of ocean acidification, euxinia, and fluctuating productivity[3]. During this interval, metazoan-dominated reefs are thought to have been replaced by microbial deposits that are considered the hallmark of the Early Triassic[4–7]. Here we use field and microscopic investigations to document Early Triassic bioaccumulations and reefs from the western USA that comprise of various sponges and serpulids associated with microbialites and other eukaryotic benthic organisms. These metazoan-rich reefs were formed only 1.5 million years after the extinction, in contrast to previous suggestions of a much delayed recovery of complex benthic communities. We conclude that the predominance of microbial reefs following the mass extinction is restricted to short intervals of the earliest Triassic. We suggest that metazoan reef building continued throughout the Early Triassic wherever permitted by environmental conditions.

Contrasting with a delayed recovery paradigm, mostly derived from diversity patterns of benthic organisms (for example, bivalves, gastropods), recent analyses on nekto-pelagic taxa such as ammonoids and conodonts document an explosive Early Triassic rediversification within less than 2 million years (Myr) after the Permian–Triassic (PT) crisis[8,9]. Nevertheless, metazoan reefs (see Supplementary Information for definition) formed by organisms such as sponges or corals are still acknowledged to re-establish during the Middle Triassic[10–12]. Their reappearance often serves as marker for the end of the recovery. Indeed, reports of well-dated Early Triassic metazoan reef builders have been exceptional (Fig. 1). Sponge concentrations are known from the Spathian of Utah and Nevada[13,14]. Small bivalve bioherms and a stromatolite–sponge–*Tubiphytes* association are recognized in the Spathian of Nevada[15,16], and a stromatolite–sponge association is known from the late Lower Triassic of the Germanic basin[17]. Some isolated bryozoans and calcareous algae are also reported[18,19]. Despite these rare occurrences, a global Early Triassic metazoan reef gap seems remarkable. This gap is often interpreted as the outcome of combined persistent or intermittent harsh environmental conditions and exacerbated biotic competitive pressures[6,20].

Here we present new evidence for large, *in situ* Early Triassic metazoan bioaccumulations and reefs formed by various sponges and serpulids associated with different microbial carbonates and eukaryotic organisms (Fig. 1; Supplementary Fig. S1). The oldest metazoan bioaccumulations and reefs are located near the base of the Thaynes Group in sections of the Pahvant Range (PR) and the Mineral Mountains (MM; Fig. 2). Ammonoid and conodont biostratigraphy indicates an early Smithian age for these levels, occurring within the '*Meekoceras* n. sp. 1 and 2 beds' and below the '*Radioceras* aff. *evolvens* bed' for the PR, and within the '*Vercherites* aff. *pulcher* bed' for the MM. U/Pb calibration of the ammonoid zonation indicates that they postdate the PT boundary by only ~1.5 Myr[2].

In the PR, the oldest reefs consist of small (~5 mm) sponges encrusting thin bivalve shell layers (Figs 2i, 3a), which probably facilitated their settlement and enhanced their preservation. Although these sponges are preserved in life position, their initial essentially globular shape now seems compacted (Supplementary Fig. S2). The sponges are associated with small serpulids within a very abundant micritic matrix, and with common echinoderm plates (probably crinoids) locally reworked as bioclastic accumulations in storm-induced deposits. These biostromes, tens of centimetres thick, are formed by alternating gregarious settling and hydraulic reworking. The latter leads to multiple short-term events of hard-part concentrations in a low to moderate energy mid ramp environment. Isolated sponges are also found within overlying beds, identified only by sparse bundles of spicules. Sponges occur a few metres higher in recurrent large (~50 m of lateral exposure) lenticular ~5-cm-thick layers, throughout a ~20 m-thick stratigraphic interval (Figs 2ii, 3b,c; Supplementary Figs S4–S6). These sponges are preserved *in situ* as lenticular reefs composed of small coalesced spheres (≤1 cm in diameter) that resemble lyssacine hexactinellids bound by submillimetre-scale biofilms. Within the lowermost Spathian PR beds, serpulids form small millimetre to centimetre-consortia with abundant ostracods, brachiopods and rare gastropods, alternating with tempestite deposits (Fig. 2iii; Supplementary Fig. S7).

Early Smithian reef deposits in the MM are characterized by more diverse sponge morphologies (Figs 2iv–v, 3d–h; Supplementary Figs S8–S22). The oldest sponges are embedded within microbialites forming reefs, tens of centimetres thick, distributed throughout a massive (up to 10 m high) microbial carbonate unit. These microbialites are composed of centimetre-scale stromatolitic domes and thrombolites sealed off by micrite. Complete cup- to flat-shape and dendroid centimetre-scale sponges are preserved, resting on micrite matrix or encrusting microbialitic crusts. They show an internal re-crystallized spiculitic network and are often

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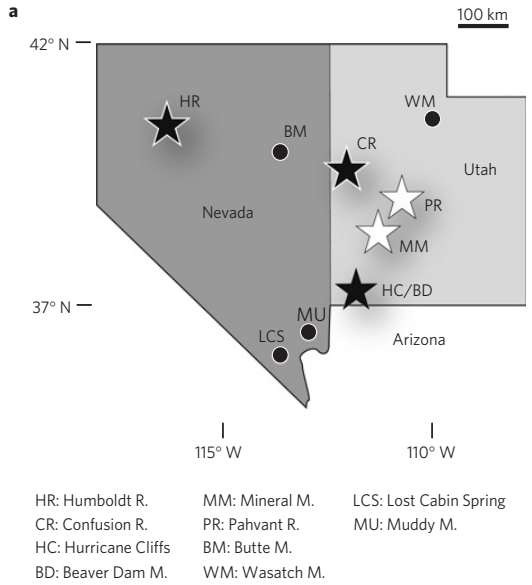

Figure 1 | Geographic and temporal overview of the studied Early Triassic bioaccumulations and reefs from western USA. a, Present-day location. White and black stars indicate Smithian and Spathian outcrops, respectively (R.: Range; M.: Mountains); black circles indicate previously described Spathian bivalve bioherms in the Muddy Mountains (ref. 15), sponge reef in Lost Cabin Spring (ref. 16), and sponge occurrences in the Butte Mountains and Wasatch Mountains (ref. 14). **b**, Early Triassic timescale in Myr with simplified global $\delta^{13}C$ trend (both adapted from ref. 2). New reefs reported in this study are symbolized by grey circles.

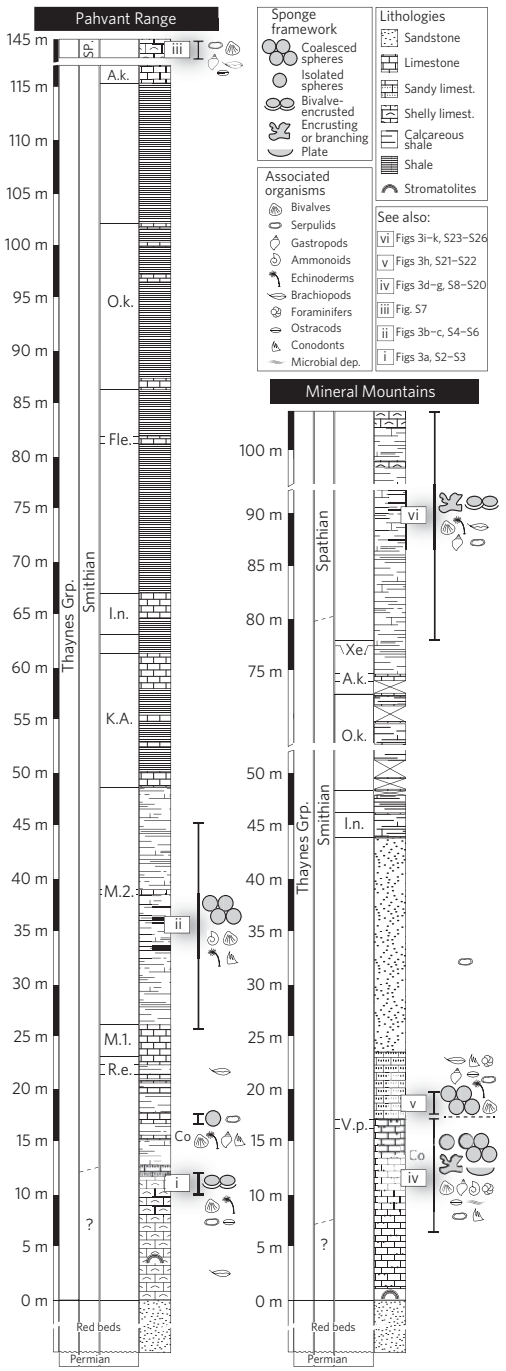

Figure 2 | Simplified litho- and biostratigraphy for the PR and MM sections. Bioaccumulations and reefs with associated benthic and nekto-pelagic organisms. Ammonoid-based biostratigraphy: Xe., *Glyptophiceras-Xenoceltites* beds; A.k., *Anasibirites kingianus* beds; O.k., *Owenites koeneni* beds; Fle., *Flemingites* beds; I.n., *Inyoites* n. sp. beds; K.A., *Kashmirites-Arctoceras* beds; M.2., *Meekoceras* n. sp.2 bed; M.1., *Meekoceras* n. sp.1 beds; R.e., *Radioceras* aff. *evolvens* bed; V.p., *Vercherites* aff. *pulcher* bed. Co: oldest occurrence of the Smithian conodont *Furnishius triserratus*. Sp.: Spathian. Reefs and bioaccumulations are indicated by the symbols i-vi with a key at the top right to the associated figures in the main paper and the Supplementary Fig. denoted by S.

partially to completely dissolved and replaced by calcite-cemented cavities (Fig. 3e; Supplementary Fig. S10). Within the uppermost part of this unit, some cylindrical or branching, imbricated calcite-cemented cavities reach sizes of tens of centimetres. Their external wall contacts are fringed by a complex network made of regular, successive lined micritic pores or larger sprout-like

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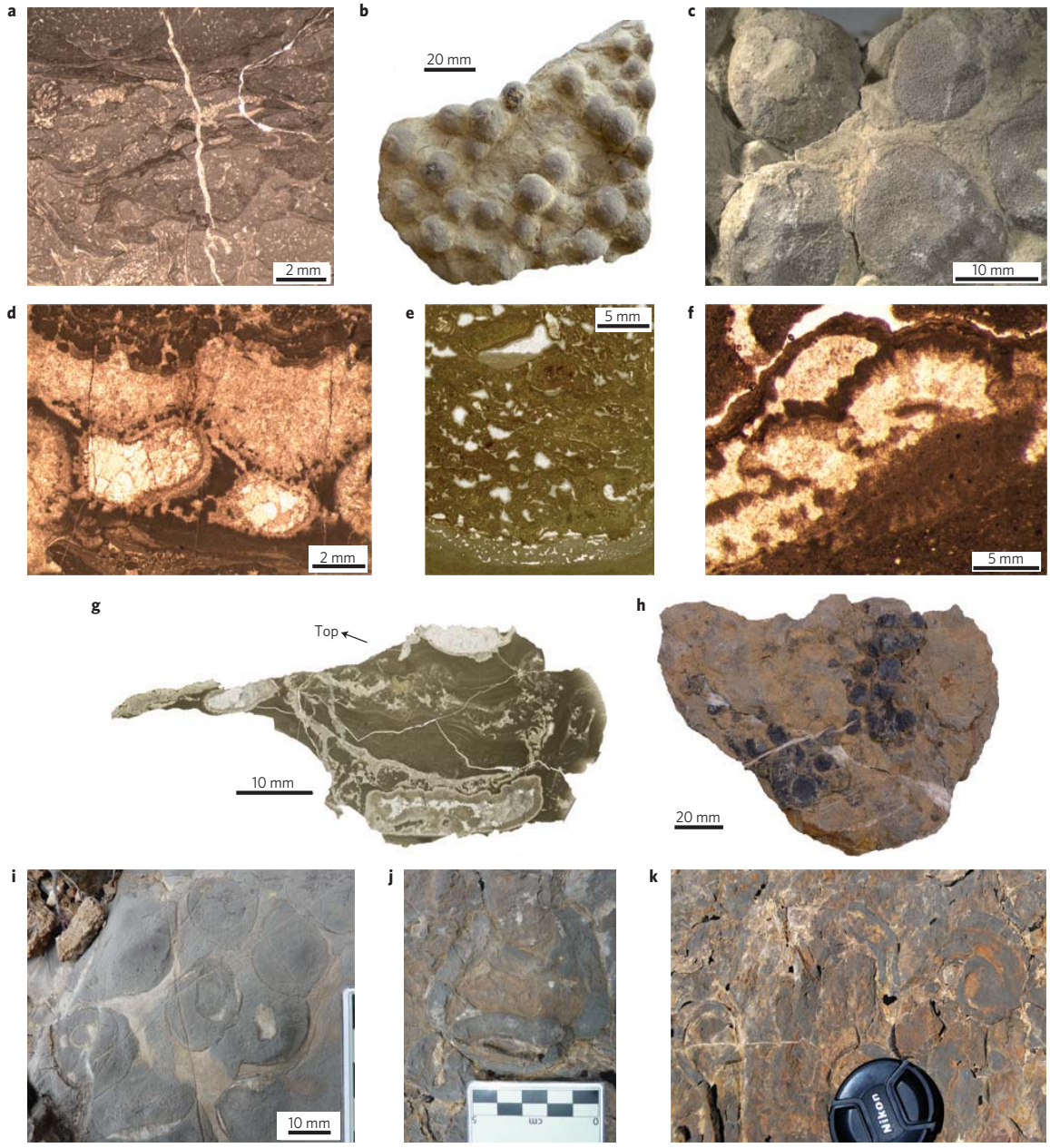

Figure 3 | Most characteristic features of sponge bioaccumulations or reefs i-ii and iv–vi. a, Abundant sponges encrusting bivalves. **b**,**c**,**h**, Coalesced spheroid sponges identified as lyssacine hexactinellids. **d**–**g**, Cavities, chambers or *in situ* spiculitic networks of various incrusting, planar and branched sponges. **i**–**k**, Sponges encrusting bivalves co-occurring with lenticular to irregular sponge structures with centimetre-thick walls. The key to the levels is given in Fig. 2. Level iii is illustrated in Supplementary Fig. S7.

openings and early cements (Supplementary Figs S13, S17–S18), closely resembling hypercalcified sponge structures[21]. Some sponges clearly showing interconnected, superimposed chambers can be assigned to sphinctozoan demosponges (Supplementary Fig. S15). Isolated or clustered spheroid sponges similar to the PR also occur in this part of the section. However, one spheroid specimen differs by its internal thick labyrinthine structure (Supplementary Fig. S14) and might be assigned to Calcarea. Therefore, at least two different classes of sponges (Demospongiae and Hexactinellida) are identified within the same reef exhibiting different morphologies, thus supporting a multi-species sponge community. Associated organisms include various foraminifers, common gastropods, bivalves, serpulids, ammonoids, abundant ostracods, brachiopods, echinoderms (crinoids and rare urchin spines) and conodonts (Fig. 2iv–v; Supplementary Figs S8–S22). Combined interstitial microbial structures are composed of flat to slightly undulating dark laminae (up to 1 cm thick) with peloids, bounding fenestral-dominant and oncoid–ooid grainstones. Microbialites are frequently reworked under tidal wave influence in clast and centimetre-ooid/oncoid-rich levels (Supplementary Fig. S11). Changes in microbialite morphology, weak organism reworking, complete large sponges and a decrease in ooid–oncoid grainstones

indicate variations from high energy inner ramp to moderate energy mid ramp domains, enhancing the settlement and development of sponges tens of centimetres thick (Supplementary Fig. S30).

In the MM section, the upper sponge-rich layers are latest Smithian and early Spathian in age (top of and above the '*Glyptophiceras-Xenoceltites* beds'; Figs 2vi, 3i–k; Supplementary Figs S23–S26). They are similar to the lower Smithian PR reef, showing a lenticular and sporadic distribution over a total thickness of ~15 m. These buildups contain centimetre-scale globular sponges in life-position, encrusting bivalve shells embedded in mud deposited in low to moderate energy environments. Locally, sponges are accompanied by abundant gastropods, brachiopods and moderately common serpulids. Overlying layers contain tens of centimetres thick rolled up, cup-like and branching sponges organized in metre-thick buildups exhibiting flat and dome shapes (Fig. 3j,k; Supplementary Fig. S23). Internal sponge structures are usually poorly preserved and microsparitized.

Furthermore, new Spathian sponge bioaccumulations and reefs are reported from the Hurricane Cliffs (HC), Beaver Dam (BD) and Humboldt Range (HR) sections (Fig. 1; Supplementary Figs S27–S28). Based on ammonoids, they are early and middle Spathian in age (HC, BD: *Tirolites* sp. beds; HR: *Prohungarites gustadti* beds). Similar to the early Smithian of the PR, sponges (probably lyssacine hexactinellids) are also preserved as small and densely coalesced spheres up to ~2 cm in diameter, showing a lenticular distribution. We also resampled different sponge accumulations from the Confusion Range (CR; Supplementary Fig. S29). Based on ammonoids, they begin in the early Spathian (*Columbites* beds) and contain abundant hexactinellid *Cypellospongia fimbriartis*[13,14] associated with diverse and abundant organisms, including coiled and orthoconic nautiloids, ammonoids, bivalves and crinoids. These highly size-variable sponges (few mm up to >30 cm) exhibit goblet-like to platter-like morphologies.

These occurrences of *in situ* sponge, sponge–bivalve and sponge–microbe–bivalve–serpulid consortia associated with diversified benthic and nekto-pelagic faunas provide new insights into the Early Triassic metazoan 'reef gap'. Indeed, the oldest metazoan reefs illustrated here occur ~1.5 Myr after the PT boundary, thus drastically shortening the duration of the gap. The tacitly acknowledged exclusive contribution of microbes as main reef builders during the Early Triassic is challenged by these metazoan bioaccumulations and reefs covering large areas within inner/outer ramp settings. Differing from previously described latest Early Triassic bivalve bioherms[15], these transient reefs and benthic communities are ecologically more complex, showing diverse built structures and organism interactions as well as tightly associated growths of their components. Although the pre-extinction diversity of sponges is not reached, different new taxa and morphologies pertaining to various classes are here reported for the Early Triassic, where a single one was previously documented[13,14].

These new findings profoundly alter the timing of the microbe-dominated benthic communities as well as reef reorganization models after the PT mass extinction[10,22,23]. It is often hypothesized that the large Early Triassic carbon cycle perturbations are linked with deleterious global oceanic conditions leading to a delayed biotic recovery, at least up to the Spathian, when the amplitude and the number of fluctuations decreased[2,3]. However, the reefs described here occur significantly earlier (Fig. 1b), indicating that temporary favourable conditions (absence of anoxic, euxinic or acidic waters) for a broad array of physiologically diverse organisms had already returned, at least regionally. Hence, the Early Triassic metazoan 'reef gap' may be better described as a reef low from which a selective preservation bias and insufficient sampling efforts still need to be factored out. The wide distribution of metazoan reefs within eastern Panthalassic equatorial palaeolatitudes also brings a different perspective to the large-scale palaeobiogeographic recovery patterns of the benthos with respect to previous claims of an earlier recovery within the mid/high palaeolatitudes[24].

Heterozoans dominate these new benthic communities, among which filter-feeding and usually stress-tolerant sponges, together with serpulids are the main metazoan builders. Such diversified communities probably benefited from varied and abundant food sources and adequate nutrient input from continental weathering and/or regional oceanic currents and sea-level rise[25]. During the early Smithian, nutrient fluxes and productivity were effective enough to sustain the development of these bioaccumulations and reefs. This is in agreement with a previous hypothesis favouring a rapidly restored, diversified primary productivity after the PT crisis[8]. Ultimately, once re-established, this community, including microbial deposits, was directly affected by water depth and current/wave energy (Supplementary Fig. S30).

Sponge–microbe reefs are not exceptional in the geological record[20,25]. However, some of these new Early Triassic sponges are morphologically different from those of classical Late Permian reefs but closer to other Mesozoic forms. Therefore, they do not suggest a local survival in climatic or depth refuges but rather the formation of a new reef ecology with different actors and roles. Similar associations are also known in the immediate aftermath of other mass extinctions[26,27], showing that only a short time interval is required to rebuild new reefal communities, even if the main builders differ from pre-crisis assemblages.

The absence of corals, or their failure to calcify[28], remains remarkable for the Early Triassic[11] and contrasts with their flourishing in later Triassic times. The absence could be due to the impossibility for these stenotypic reef builders to cope with intermittent deleterious conditions. Furthermore, high temperatures could have been a potential cause for the lack of heavily calcified organisms, as they physiologically influence calcification[11]. However, temperatures probably fluctuated strongly during the Early Triassic[2]. Lowered pH, low O_2 and high H_2S concentrations triggered by the Siberian Traps[2,29] may all have contributed to the temporary absence of heavily calcified organisms. However, the intense production of $CaCO_3$ tests among Smithian and Spathian heterozoan communities from the western USA, as well as abundant microbialites and micrite mud support a high calcite saturation[6].

Ultimately, the observed proliferation of sponges predating the supposed main recovery phase of the siliceous zooplankton[30] raises the question of the duration and intensity of the Early Triassic 'chert gap'. Clearly, our results also call for an in-depth reappraisal of the biotic and abiotic limiting factors for silica biomineralization in the Early Triassic Ocean.

Methods summary

The two main sections studied are located in the PR and the MM of Utah (Fig. 1; Supplementary Fig. S1). We also report new early and middle Spathian metazoan buildups formed by sponges from the Hurricane Cliffs (HC; Utah), Beaver Dam Mountains (BD; Utah) and Humboldt Range (HR; Nevada), as well as various bioaccumulations of sponges from the early Spathian of the Confusion Range (CR; Utah). ~300 samples were collected bed-by-bed from these sections. Variably oriented polished slabs and thin sections were prepared from each sample and we chose the best preserved metazoan builders for cathodoluminescence analyses. Thin sections were observed by means of natural and polarized light microscopy using a Leica M205C binocular microscope coupled with a Leica DFC295 digital camera.

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References

1. Erwin, D. H. *Extinction. How life on Earth Nearly Ended 250 Million Years Ago* (Princeton Univ. Press, 2006).
2. Galfetti, T. *et al.* Timing of the Early Triassic carbon cycle perturbations inferred from new U–Pb ages and ammonoid biochronozones. *Earth Planet. Sci. Let.* **258,** 593–604 (2007).
3. Payne, J. L. *et al.* Large perturbations of the carbon cycle during recovery from the end-Permian extinction. *Science* **305,** 506–509 (2004).

4. Baud, A., Richoz, S. & Pruss, S. The Lower Triassic anachronistic carbonate facies in space and time. *Global Planet. Change* **55,** 81–89 (2007).
5. Pruss, S. B., Bottjer, D. J., Corsetti, F. A. & Baud, A. A global marine sedimentary response to the end-Permian mass extinction: Examples from southern Turkey and the western United States. *Earth Sci. Rev.* **78,** 193–206 (2006).
6. Woods, A. D. Anatomy of an anachronistic carbonate platform: Lower Triassic carbonates of the southwestern United States. *Aust. J. Earth Sci.* **56,** 825–839 (2009).
7. Woods, A. D. & Baud, A. Anachronistic facies from a drowned Lower Triassic carbonate platform: Lower member of the Alwa Formation (Baïd Exotic), Oman Mountains. *Sediment. Geol.* **209,** 1–14 (2008).
8. Brayard, A. *et al.* Good genes and good luck: Ammonoid diversity and the end-Permian mass extinction. *Science* **325,** 1118–1121 (2009).
9. Orchard, M. J. Conodont diversity and evolution through the latest Permian and Early Triassic upheavals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **252,** 93–117 (2007).
10. Weidlich, O., Kiessling, W. & Flügel, E. Permian–Triassic boundary interval as a model for forcing marine ecosystem collapse by long-term atmospheric oxygen drop. *Geology* **31,** 961–964 (2003).
11. Payne, J. L., Lehrmann, D. J., Christensen, S., Wei, J. & Knoll, A. Environmental and biological controls on the initiation and growth of a Middle Triassic (Anisian) reef complex on the Great Bank of Guizhou, Guizhou Province, China. *Palaios* **21,** 325–343 (2006).
12. Flügel, E. in *Phanerozoic Reef Patterns* Vol. 72 (eds Kiessling, W., Flügel, E. & Golonka, J.) 391–463 (SEPM Special 26 Publication Series, Society for Sedimentary Geology, 2002).
13. Pisera, A., Rigby, J. K. & Bylund, K. G. Lower Triassic hexactinellid sponges from the Confusion Range, western Utah. *BYU Geol. Stud.* **41,** 139–148 (1996).
14. Rigby, J. K. & Gosney, T. C. First reported Triassic lyssakid sponges from North America. *J. Paleontol.* **57,** 787–796 (1983).
15. Pruss, S. B., Payne, J. L. & Bottjer, D. J. *Planucopsis* bioherms: The first metazoan buildups following the end-Permian mass extinction. *Palaios* **22,** 17–23 (2007).
16. Griffin, J. M., Marenco, P. J., Fraiser, M. L. & Clapham, M. E. *2010 GSA Annual Meeting* Paper no. 21–16 (Denver, 2010).
17. Szulc, J. in *The Global Triassic* Vol. 41 (eds Lucas, S. G. & Spielmann, J. A.) (New Mexico Museum of Natural History, 2007).
18. Baud, A., Brandner, R. & Donofrio, D. A. The Sefid Kuh Limestone—A late Lower Triassic carbonate ramp (Aghdarband, NE-Iran). *Abh. Geol. B. –A.* **38,** 111–123 (1991).
19. Baud, A. *et al.* Lower Triassic bryozoan beds from Ellesmere Island, High Arctic, Canada. *Polar Res.* **27,** 428–440 (2008).
20. Riding, R. Microbial carbonate abundance compared with fluctuations in metazoan diversity over geological time. *Sediment. Geol.* **185,** 229–238 (2006).
21. Senowbari-Daryan, B., Caruthers, A. H. & Stanley, G. D. Jr The First Upper Triassic Silicified Hypercalcified Sponges from the Alexander Terrane, Gravina Island and Keku Strait, Southeast Alaska. *J. Paleontol.* **82,** 344–350 (2008).
22. Pruss, S. B. & Bottjer, D. J. The reorganization of reef communities following the end-Permian mass extinction. *C. R. Palevol* **4,** 553–568 (2005).
23. Schubert, J. K. & Bottjer, D. J. Early Triassic stromatolites as post-mass extinction disaster forms. *Geology* **20,** 883–886 (1992).
24. Twitchett, R. J. & Barras, C. J. *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis* 397–418 (Geological Society Special Publication, 2004).
25. Brunton, F. R. & Dixon, O. A. Siliceous sponge-microbe biotic associations and their recurrence through the Phanerozoic as reef mound constructors. *Palaios* **9,** 370–387 (1994).
26. Wood, R. Palaeoecology of a post-extinction reef: Famennian (Late Devonian) of the Canning Basin, North-western Australia. *Palaeontology* **47,** 415–445 (2004).
27. Delecat, S. & Reitner, J. Sponge communities from the Lower Liassic of Adnet (Northern Calcareous Alps, Austria). *Facies* **51,** 385–404 (2005).
28. Stanley, G. D. Jr The evolution of modern corals and their early history. *Earth Sci. Rev.* **60,** 195–225 (2003).
29. Knoll, A. H., Bambach, R. K., Payne, J. L., Pruss, S. & Fischer, W. W. Paleophysiology and end-Permian mass extinction. *Earth Planet. Sci. Lett.* **256,** 295–313 (2007).
30. O'Dogherty, L., Carter, E. S., Š Goričan, Š. & Dumitrica, P. Triassic radiolarian biostratigraphy. *Geol. Soc. Lond. Spec. Publ.* **334,** 163–200 (2010).

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Author contributions

Fieldwork was carried out by all authors. Thin section studies were performed by E.V., A.B. and N.O. Ammonoid determinations: A.B. and H.B. Conodont determinations: N.G. Manuscript was written by A.B., E.V., N.O, G.E., H.B. with comments on contents from all authors.

Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on www.nature.com/naturegeoscience. Reprints and permissions information is available online at http://www.nature.com/reprints. Correspondence and requests for materials should be addressed to A.B.

IV Faunal lists

A. Faunal list and absolute abundances of the Virgin Formation (chapter 2)

Species	Samples													
	BD-A-4	BD-A-6	HC-A-1	VR-1	BD-A-7	BD-A-5	BD-B-1	BD-B-0	VR-2	BD-A-3	HC-B-1	HC-C-1	HC-B-4	HC-D-7
Astartidae sp. A	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Bakevellia costata	0	0	1	1	8	1	0	7	0	8	0	0	5	37
Bakevellia exporrecta	103	25	12	7	0	0	7	19	0	34	0	2	0	0
Eumorphotis cf. *venetiana*	1	0	0	0	4	1	0	11	0	0	0	0	6	0
Eumorphotis cf. *multiformis*	5	0	0	6	5	0	0	3	3	0	0	3	0	1
Eumorphotis ericius	3	0	0	12	36	9	21	9	35	31	0	1	0	0
Eumorphotis virginensis	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Leptochondria curtocardinalis	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Leptochondria nuetzeli	41	40	0	5	4	0	0	0	0	14	0	0	0	0
Myalinella sp. A	0	0	0	0	6	0	0	0	0	1	0	0	0	0
Neoschizodus laevigatus	0	0	0	5	0	0	0	0	3	0	0	0	0	0
Pernopecten sp. A	0	0	0	0	5	1	0	0	1	0	0	0	0	0
Promyalina putiatinensis	3	0	11	9	10	2	40	7	39	5	0	0	1	0
Promyalina spathi	0	0	0	0	0	0	0	0	0	0	0	0	0	15
Protopis sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Sementiconcha recuperator	89	0	0	0	0	0	0	3	1	19	0	0	0	0
Trigonodus cf. *sandbergi*	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Trigonodus cf. *orientalis*	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Unionites canalensis	1	0	0	0	1	0	0	0	0	0	0	0	0	0
Unionites fassaensis	2	0	0	0	1	0	0	3	2	4	0	0	0	0
Natiria cf. *costata*	0	0	0	0	0	0	0	2	0	2	0	0	0	0
Gastropod ind. sp. A	0	0	1	0	1	0	0	6	0	1	0	1	0	0
Piarorhynchella triassica	4	0	0	0	4	1	100	24	31	2	20	97	0	0
Protogusarella smithi	0	0	0	0	12	0	400	50	48	59	5	2	0	0
Ammonoid ind. sp. A	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Tirolites sp. A	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Ammonoid ind. sp. B	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Cypellospongia sp. A	0	0	0	0	7	2	0	0	0	0	0	0	0	0
Holocrinus smithi	0	0	0	c	c	c	0	r	c	0	r	0	c	0
Miocidaris utahensis	0	0	0	r	a	c	r	vr	c	0	c	r	0	0

r - rare, vr - very rare, c - common, a - abundant

B. Faunal list and absolute abundances of the Dinwoody Formation (chapter 3)

Species	Samples													
	LPA-2	CM	GV-B-B	GV-B-1	GV-B-2	GV-B-3	GV-B-4	GV-A-1	GV-A-2	GV-A-3	GV-A-4	GV-A-5	GV-A-7	GV-A-8
Promyalina putiatinensis	12	0	0	0	0	0	0	0	0	3	0	0	0	0
Promyalina spathi	10	8	0	1	0	0	0	0	0	1	1	1	0	0
Unionites canalensis	6	0	0	0	7	0	0	0	0	15	2	2	0	0
Neoschizodus laevigatus	0	0	0	0	0	0	0	0	0	2	0	5	0	0
Pteria ussurica	29	0	0	0	0	23	134	0	0	1	0	43	45	67
Unionites fassaensis	62	17	0	46	70	17	1	35	21	2	57	57	0	7
Claraia cf. stachei	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Claraia mulleri	0	0	0	1	0	0	0	0	0	0	0	5	0	0
Claraia aurita	0	10	0	0	0	0	0	0	0	0	0	0	0	0
Leptochondria occidanea	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Eumorphotis amplicostata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eumorphotis multiformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myalinella postcarbonica	1	3	0	0	0	0	0	0	0	0	0	0	0	1
Permophorus bregeri	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eumorphotis cf. *ericius*	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coelostylina sp. A	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Dicellonema abrekensis	38	0	0	0	0	0	0	0	0	0	0	0	0	0
Lingula borealis	0	12	46	0	0	0	0	0	0	0	0	0	0	0
Periallus woodsidensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Species	Samples										
	LS-4/a	LS-5/a	LS-5/b	LS-7	TM-1	TM-2	TM-3	TM-4	TM-9	TM-(8/9)	TM-12
Promyalina putiatinensis	0	0	0	0	0	0	0	0	0	0	0
Promyalina spathi	3	4	12	13	0	0	0	0	0	0	1
Unionites canalensis	4	1	2	0	0	0	0	0	0	0	0
Neoschizodus laevigatus	0	0	0	0	0	0	0	0	0	0	0
Pteria ussurica	6	0	0	1	0	0	0	0	0	0	0
Unionites fassaensis	73	3	13	2	0	0	0	2	0	0	0
Claraia cf. stachei	0	0	0	0	0	0	0	0	0	0	0
Claraia mulleri	0	0	0	0	0	0	0	0	0	0	0
Claraia aurita	0	0	0	0	0	0	0	0	0	0	0
Leptochondria occidanea	19	0	0	0	6	1	3	1	1	8	0
Eumorphotis amplicostata	0	0	2	1	0	0	0	0	0	0	0
Eumorphotis multiformis	0	0	37	72	0	0	1	1	0	0	0
Myalinella postcarbonica	0	0	0	0	0	0	0	0	0	0	0
Permophorus bregeri	0	0	0	0	0	0	0	0	0	0	0
Eumorphotis cf. *ericius*	0	0	3	28	0	0	0	0	0	0	0
Coelostylina sp. A	0	0	0	12	0	0	0	0	0	0	0
Dicellonema abrekensis	0	0	0	0	0	0	0	0	0	0	0
Lingula borealis	72	139	21	12	0	0	0	0	0	0	0
Periallus woodsidensis	0	0	0	0	0	0	0	9	0	2	0

Species	Samples									
	HS	HS-1	HS-L-1	SC-1/L	SC-1	HP-1	HP-3	HP-5	HP-2L	HP-13
Promyalina putiatinensis	0	0	0	0	0	0	0	0	0	0
Promyalina spathi	0	0	0	0	0	0	0	0	2	0
Unionites canalensis	0	0	0	0	0	1	0	0	0	0
Neoschizodus laevigatus	0	0	0	0	0	0	0	0	0	0
Pteria ussurica	0	0	0	1	0	3	0	0	1	0
Unionites fassaensis	0	1	0	0	2	0	0	6	0	0
Claraia cf. stachei	0	0	0	0	0	0	0	0	0	0
Claraia mulleri	0	0	0	0	0	0	0	0	0	0
Claraia aurita	0	0	0	0	0	0	0	0	0	0
Leptochondria occidanea	0	0	0	0	0	0	0	0	0	0
Eumorphotis amplicostata	0	0	0	0	0	0	0	8	3	0
Eumorphotis multiformis	0	0	4	0	3	0	3	17	17	0
Myalinella postcarbonica	8	0	0	0	0	0	0	0	0	0
Permophorus bregeri	21	0	0	0	0	0	0	0	0	0
Eumorphotis cf. *ericius*	0	0	0	0	0	0	0	0	0	0
Coelostylina sp. A	3	0	0	0	0	0	0	0	0	0
Dicellonema abrekensis	0	0	0	0	0	0	0	0	0	0
Lingula borealis	0	0	0	0	0	55	50	0	0	48
Periallus woodsidensis	0	0	0	0	0	0	0	0	0	0

C. Faunal list and absolute abundances of the Sinbad Formation (chapter 4)

Species	Samples										
	TO-A-1	TO-A-2	TO-A-3	TO-A-4	TO-A-5	TO-A-6	SR-1	SR-2	SR-3	SR-4	SR-5
Confusionella loczyi	17	8	9	0	0	0	5	2	0	0	0
Leptochondria occidanea	15	9	2	1	37	21	0	12	5	0	0
Leptochondria xijinwulanensis	7	1	2	0	0	0	0	0	2	0	0
Eumorphotis cf. *beneckei*	0	0	0	0	0	0	0	0	0	0	0
Eumorphotis multiformis	0	0	0	0	0	0	1	0	0	0	0
Eumorphotis hinnitidea	0	0	0	0	0	0	0	0	0	0	0
Eumorphotis ericius	0	0	0	0	0	0	0	0	0	0	0
Promysidiella sp. A	39	2	0	0	0	29	28	129	57	58	9
Crittendenia? sp. A	0	0	0	0	0	0	2	1	1	0	0
Unionites cf. *canalensis*	5	0	0	0	0	0	0	0	0	1	0
Unionites cf. *fassaensis*	1	0	0	2	0	0	0	2	0	0	0
Unicardium sp. A	0	0	0	0	0	0	0	0	0	0	0
Permophorus cf. *bregeri*	0	0	0	0	0	0	0	0	0	17	2
Neoschizodus laevigatus	0	0	0	0	0	7	0	0	0	1	0
Sinbadiella pygmaea	2	0	0	0	0	0	0	3	0	0	0
Sementiconcha recuperator	0	0	0	0	0	0	0	0	0	1	0
Bakevellia cf. *exporrecta*	1	0	0	0	1	5	0	1	0	1	0
Pernopecten sp. A	0	0	0	3	2	0	0	0	0	0	0
Polygyrina sp. A	3	13	0	0	0	0	0	1	6	0	0
Strobeus batteni	0	0	0	0	0	0	0	0	0	0	0
Abrekopsis cf. *depressispirus*	1	1	1	1	2	0	0	33	19	1	13
Laubopsis ? sp. A	0	0	0	0	0	0	0	0	0	0	0
Neritaria costata	0	0	0	0	0	0	0	0	0	1	0
Worthenia windowblindensis	0	0	0	0	0	0	0	0	0	0	0
Chartronella ? sp. A	3	0	0	0	0	0	2	6	1	0	0
Lingularia borealis	0	0	0	0	0	0	0	0	0	0	0
Obnixia thaynesiana	0	0	0	0	0	0	0	0	0	0	0

D. Faunal list and absolute abundances of the Thaynes Group (chapter 4)

Species	Samples														
	MV-2	MV-3	MV-4	MV-5	MV-6	MV-7	MV-8	MV-9	MV-10	MV-11	MV-12	DV-1	DV-2	DV-3	DV-5
Confusionella loczyi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Leptochondria occidanea	0	2	3	0	0	0	1	0	7	1	0	0	0	0	2
Leptochondria xijinwulanensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eumorphotis cf. *beneckei*	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Eumorphotis multiformis	0	1	0	2	3	0	0	0	16	0	0	0	15	0	0
Eumorphotis hinnitidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eumorphotis ericius	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0
Promysidiella sp. A	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0
Crittendenia? sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Unionites cf. *canalensis*	0	0	0	0	0	0	0	0	0	0	0	16	3	0	0
Unionites cf. *fassaensis*	0	4	1	0	0	0	0	0	0	0	0	1	0	0	0
Unicardium sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Permophorus cf. *bregeri*	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0
Neoschizodus laevigatus	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0
Sinbadiella pygmaea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sementiconcha recuperator	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bakevellia cf. *exporrecta*	0	10	9	1	0	9	0	28	1	0	17	0	0	0	0
Pernopecten sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygyrina sp. A	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Strobeus batteni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Abrekopsis cf. *depressispirus*	45	0	0	0	0	0	0	0	0	0	0	0	0	6	0
Laubopsis? sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neritaria costata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Worthenia windowblindensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chartronella? sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lingularia borealis	0	0	0	0	0	0	0	0	0	0	0	6	4	0	0
Obnixia thaynesiana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Species	Samples												
	CP-0	CP-1	CP-2	CP-3	CP-4	CP-5	CP-101	CP-102	CP-7	CP-8	DH-3-1	DH-3-2	DH-3-3
Confusionella loczyi	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptochondria occidanea	0	13	0	1	0	0	0	0	13	26	1	0	0
Leptochondria xijinwulanensis	0	0	0	0	0	0	0	0	0	0	0	0	0
Eumorphotis cf. *beneckei*	0	0	0	0	0	0	0	0	0	0	0	0	0
Eumorphotis multiformis	0	0	0	0	0	0	0	0	0	0	2	0	1
Eumorphotis hinnitidea	0	0	0	0	1	0	0	0	0	0	0	0	0
Eumorphotis ericius	0	0	16	27	12	34	4	0	0	0	0	0	0
Promysidiella sp. A	0	0	0	0	0	0	3	0	0	0	0	0	0
Crittendenia? sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Unionites cf. *canalensis*	0	0	0	8	0	0	0	0	0	0	0	0	0
Unionites cf. *fassaensis*	0	0	0	0	0	0	0	0	0	0	1	0	0
Unicardium sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Permophorus cf. *bregeri*	0	0	0	0	0	0	0	0	0	0	0	0	0
Neoschizodus laevigatus	0	0	0	0	0	0	0	0	0	0	0	0	0
Sinbadiella pygmaea	0	0	0	0	0	0	0	0	0	0	0	0	0
Sementiconcha recuperator	0	0	0	0	0	0	0	0	0	0	0	0	0
Bakevellia cf. *exporrecta*	57	0	0	9	37	0	4	0	0	0	4	69	0
Pernopecten sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygyrina sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Strobeus batteni	0	0	0	0	0	0	0	0	0	0	0	0	0
Abrekopsis cf. *depressispirus*	0	0	0	0	0	0	0	0	0	0	0	0	0
Laubopsis? sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Neritaria costata	0	0	0	0	0	0	0	0	0	0	0	0	0
Worthenia windowblindensis	0	0	0	0	0	0	0	0	0	0	0	0	0
Chartronella? sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Lingularia borealis	0	0	0	0	0	0	0	0	0	0	1	0	0
Obnixia thaynesiana	0	0	0	0	0	0	0	21	0	0	0	0	0

Species	Samples												
	DH-1-0	DH-1-0a	DH-1-1a	DH-1-2	DH-1-3	gs1	DH-1-4	DH-1-5	gs2	DH-1-8	DH-1-9	DH-1-10	DH-1-12
Confusionella loczyi	22	34	2	11	21	7	4	94	6	0	109	0	132
Leptochondria occidanea	10	1	2	9	103	3	3	0	0	1	9	3	14
Leptochondria xijinwulanensis	0	0	0	0	1	0	0	2	0	0	1	0	0
Eumorphotis cf. *beneckei*	1	0	0	1	0	0	0	1	0	0	0	0	0
Eumorphotis multiformis	0	0	0	0	0	0	0	0	0	0	0	0	0
Eumorphotis hinnitidea	0	0	0	0	0	0	0	0	0	0	0	0	0
Eumorphotis ericius	0	0	0	0	0	0	0	0	0	0	0	0	0
Promysidiella sp. A	0	0	0	0	0	0	0	0	0	0	2	0	0
Crittendenia? sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Unionites cf. *canalensis*	0	0	0	0	0	0	0	0	0	0	0	0	0
Unionites cf. *fassaensis*	0	0	0	0	0	0	0	0	0	0	0	0	0
Unicardium sp. A	0	0	0	0	0	0	0	0	1	0	0	0	0
Permophorus cf. *bregeri*	0	0	0	0	0	0	0	0	0	0	0	0	0
Neoschizodus laevigatus	0	0	0	0	0	0	0	0	0	0	0	0	0
Sinbadiella pygmaea	0	0	0	0	0	0	0	0	0	0	0	0	0
Sementiconcha recuperator	0	0	0	0	0	0	0	0	0	0	0	0	0
Bakevellia cf. *exporrecta*	0	0	0	0	0	0	0	0	0	0	0	0	0
Pernopecten sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygyrina sp. A	1	0	0	0	0	0	0	0	2	0	0	0	0
Strobeus batteni	0	0	0	0	0	29	0	0	22	0	1	0	0
Abrekopsis cf. *depressispirus*	0	0	0	0	0	0	0	0	0	0	0	0	0
Laubopsis? sp. A	0	0	0	0	0	11	0	0	31	0	0	0	0
Neritaria costata	0	0	0	0	0	0	0	0	0	0	0	0	0
Worthenia windowblindensis	0	0	0	0	1	0	0	0	0	0	0	0	0
Chartronella? sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Lingularia borealis	5	0	2	0	3	0	0	0	0	0	0	0	0
Obnixia thaynesiana	0	0	0	0	0	0	0	0	0	0	0	0	0

E. Faunal list and absolute abundances of the Werfen Formation (chapter 5)

Samples of the Mazzin Member

Species	Samples										
	AG-1	AG-2	AG-3	AG-4	AG-5	AG-7	AG-8	AG-9	AG-10	AG-12	AG-13
Pteria cf. *ussurica*	4	11	1	0	0	0	2	0	0	0	0
Claraia aurita	0	0	0	3	17	122	92	12	3	44	4
Eumorphotis sp. A	0	2	0	0	0	0	0	0	0	0	0
Eumorphotis multiformis	0	0	1	0	0	0	1	1	0	0	0
Neoschizodus orbicularis	0	2	0	0	0	0	4	121	0	143	0
Neoschizodus elongatus	0	0	0	0	0	0	0	0	0	0	0
Neoschizodus laevigatus	0	0	0	0	0	0	1	23	0	22	0
Towapteria scythica	0	0	0	0	0	0	25	9	0	0	0
Unionites canalensis	0	0	0	0	0	0	0	0	0	0	0
Unionites fassaensis	15	37	205	25	2	1	5	15	0	1	0
Lingula tenuissima	3	2	3	0	0	0	1	34	0	2	1
Coelostylina werfensis	2	4	2	0	3	1	0	0	0	21	0
Bellerophontid sp. A	1	15	0	0	5	0	1	0	0	0	0
Pseudomurchisonia kokeni	0	0	0	0	0	0	0	0	45	0	0

Species	Samples								
	RG-1	RG-2	RG-3	RG-4	RG-5	RG-6	RG-7	RG-8	RG-9
Pteria cf. *ussurica*	0	1	0	0	0	0	0	0	0
Claraia aurita	0	0	0	0	8	95	1	15	60
Eumorphotis sp. A	0	0	0	0	0	0	0	0	0
Eumorphotis multiformis	1	0	1	0	0	0	0	0	1
Neoschizodus orbicularis	0	0	0	0	0	0	0	0	0
Neoschizodus elongatus	0	0	0	0	0	0	0	0	0
Neoschizodus laevigatus	0	0	2	0	0	0	0	0	0
Towapteria scythica	1	0	0	0	0	1	0	0	0
Unionites canalensis	0	0	0	0	5	0	0	0	0
Unionites fassaensis	1	7	1	120	0	0	0	0	0
Lingula tenuissima	0	0	0	1	0	2	0	0	0
Coelostylina werfensis	0	6	3	0	5	0	1	0	0
Bellerophontid sp. A	0	0	0	0	0	0	0	0	0
Pseudomurchisonia kokeni	0	0	0	0	0	0	0	0	0

Samples of the Seis/Siusi Member

Species	Samples															
	AG-14	AG-15	AG-17	AG-18	AG-19	AG-20	AG-21	AG-22	AG-23	AG-25	AG-26	AG-27	AG-28	AG-29	AG-30	AG-31
Pteria cf. *ussurica*	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
Claraia aurita	0	0	0	3	6	0	1	7	7	1	2	25	0	41	2	5
Claraia clarai	18	13	42	4	2	0	0	25	0	0	0	0	0	0	0	0
Eumorphotis sp. A	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0
Eumorphotis multiformis	1	1	0	0	0	0	0	0	5	0	0	0	0	0	0	0
Neoschizodus orbicularis	0	3	5	3	9	0	0	1	1	0	2	2	0	0	0	0
Neoschizodus elongatus	0	0	0	0	0	0	0	0	0	5	0	0	0	11	0	0
Neoschizodus laevigatus	0	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unionites canalensis	0	9	4	7	35	1	0	0	12	2	0	8	0	14	1	15
Unionites fassaensis	1	0	0	2	0	1	0	1	0	0	0	0	0	0	0	0
Coelostylina werfensis	0	0	0	17	6	23	0	69	0	0	0	0	0	0	0	4
Pseudomurchisonia kokeni	0	0	0	0	0	0	0	0	0	0	0	0	60	120	0	0

Species	Samples															
	AG-32	AG-34	RG-12	RG-11	RG-13	RG-14	RG-15	RG-16	RG-17	RG-18	RG-19	RG-20	RG-21	RG-22	RG-23	RG-24
Pteria cf. *ussurica*	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0
Claraia aurita	8	0	0	1	2	1	0	2	5	3	4	7	3	0	7	5
Claraia clarai	0	0	25	1	4	3	2	7	4	0	0	0	4	1	0	0
Eumorphotis multiformis	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0
Eumorphotis cf. *hinnitidea*	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Neoschizodus orbicularis	0	0	0	0	8	1	0	0	9	0	16	0	0	0	0	0
Neoschizodus elongatus	0	0	0	0	0	0	0	0	0	0	19	1	0	0	2	0
Neoschizodus laevigatus	0	0	0	0	3	0	0	0	2	0	0	0	0	0	0	0
Stutchburia sp. A	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Unionites canalensis	0	1	4	0	12	3	1	5	6	12	0	3	4	1	2	3
Unionites fassaensis	0	0	0	0	0	3	0	11	3	0	10	0	1	1	0	0
Coelostylina werfensis	1	1	0	0	0	1	0	0	0	0	0	30	25	0	0	0
Bellerophontid sp. A	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Species	Samples							
	RG-25	RG-40	RG-41	RG-41a	RG-42	RG-43	LOP-1	LOP-2
Pteria cf. *ussurica*	0	9	0	0	0	0	0	0
Claraia aurita	5	64	7	3	14	9	8	3
Eumorphotis multiformis	1	0	0	0	0	0	0	0
Neoschizodus orbicularis	0	0	0	0	0	0	76	0
Neoschizodus elongatus	0	0	0	0	3	0	0	0
Neoschizodus laevigatus	0	0	0	0	0	0	9	0
Stutchburia sp. A	2	0	0	0	0	0	0	0
Unionites canalensis	2	31	5	2	6	2	0	24
Unionites fassaensis	0	15	18	0	5	0	15	20
Coelostylina werfensis	0	0	19	37	15	39	0	0
Pseudomurchisonia kokeni	35	0	0	0	0	0	0	0

Samples of the Gastropod Oolite Member and Campil Member

Species	Samples															
	RG-L2	RG-44	RG-45	LOP-3	LOP-4	LOP-5	LOP-6	LOP-7	LOP-L	CB-1	CB-2	CB-3	CB-4	CB-5	CB-6	CB-7
Bakevellia exporrecta	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0
Eumorphotis cf. *beneckei*	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Eumorphotis multiformis	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Neoschizodus laevigatus	0	0	0	0	13	4	18	0	0	0	0	0	0	0	0	0
Scythentolium sp. A	0	0	0	0	0	0	0	0	0	0	0	24	9	0	0	0
Unionites canalensis	0	1	3	9	2	0	0	0	6	0	0	0	0	0	0	0
Unionites fassaensis	12	21	9	3	27	21	9	87	0	7	9	0	5	1	1	9

Samples of the Val Badia and Cencenighe Member

Species	Samples															
	VV-1	VV-2	LOP-8	WH-4	WH-5	WH-6	WH-7	WH-8	WH-9	CB-9	CB-10	CB-13	CB-14	CB-15	CB-16	CB-17
Avichlamys voelseckhofensis	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Bakevellia exporrecta	7	52	1	0	0	0	0	12	2	1	0	0	1	3	0	0
Bakevellia albertii	0	3	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Costatoria subrotunda	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Eumorphotis cf. *hinnitidea*	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0
Eumorphotis telleri	0	9	1	0	0	0	0	1	2	0	0	0	0	0	1	0
Neoschizodus laevigatus	3	8	0	0	0	0	0	3	0	1	6	0	8	0	3	2
Scythentolium sp. A	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Unionites canalensis	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unionites fassaensis	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0
Werfenella rectecostata	0	0	0	2	0	5	2	1	2	0	0	0	0	0	0	0
Natiria costata	25	34	12	0	0	2	31	10	0	5	4	8	3	0	8	7
Worthenia sp. A	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Species	Samples			
	VV-3	WH-10	CB-18	CB-19
Bakevellia exporrecta	0	24	8	27
Bakevellia albertii	0	5	0	0
Eumorphotis multiformis	0	0	1	0
Eumorphotis telleri	0	8	0	0
Leptochondria alberti	0	13	0	0
Neoschizodus laevigatus	1	16	0	2
Unionites fassaensis	0	0	1	0
Praeaplocoma hessi	0	1	0	0
Werfenella rectecostata	0	8	0	0
Natiria costata	1	14	0	0

V Benthic Associations

A. Associations of the Virgin Formation (Chapter 2)

***Bakevellia exporrecta* association**						
ecology	**species/sample**	**BD-A-4**	**BD-A-6**	**HC-A-1**	**Sum**	**%**
sinf sf	*Bakevellia exporrecta*	103	25	12	**128**	40.25
inf sf	*Sementiconcha recuperator*	89	0	0	**89**	27.99
epi sf	*Leptochondria nuetzeli*	41	40	0	**81**	25.47
epi sf	*Eumorphotis* cf. *multiformis*	5	0	0	**5**	1.57
epi sf	*Piarorhynchella triassica*	4	0	0	**4**	1.26
epi sf	*Eumorphotis ericius*	3	0	0	**3**	0.94
epi sf	*Promyalina putiatinensis*	3	0	11	**3**	0.94
inf sf	*Unionites fassaensis*	2	0	0	**2**	0.63
epi sf	*Eumorphotis* cf. *venetiana*	1	0	0	**1**	0.31
inf sf	*Unionites canalensis*	1	0	0	**1**	0.31
s c	Ammonoid ind. sp. A	1	0	0	**1**	0.31
	Richness	11	2	2	11	
	Individuals	253	65	23	318	
	Dominance D	0.32	0.53	0.50	0.31	
	mean richness **8.3**			mean D **0.45**		

***Eumorphotis ericius* association**						
ecology	**species/sample**	**VR-1**	**BD-A-7**	**BD-A-5**	**Sum**	**%**
epi sf	*Eumorphotis ericius*	12	36	9	**57**	33.93
epi sf	*Promyalina putiatinensis*	9	10	2	**21**	12.50
epi sf	*Protogusarella smithi*	0	12	0	**12**	7.14
epi sf	*Eumorphotis* cf. *multiformis*	6	5	0	**11**	6.55
sinf sf	*Bakevellia costata*	1	8	1	**10**	5.95
epi sf	*Leptochondria nuetzeli*	5	4	0	**9**	5.36
epi sf	*Cypellospongia* sp. A	0	7	2	**9**	5.36
sinf sf	*Bakevellia exporrecta*	7	0	0	**7**	4.17
epi sf	*Myalinella* sp. A	0	6	0	**6**	3.57
epi sf	*Pernopecten* sp. A	0	5	1	**6**	3.57
epi sf	*Eumorphotis* cf. *venetiana*	0	4	1	**5**	2.98
inf sf	*Neoschizodus laevigatus*	5	0	0	**5**	2.98
epi sf	*Piarorhynchella triassica*	0	4	1	**5**	2.98
inf sf	Astartidae sp. A	0	0	1	**1**	0.60
inf sf	*Trigonodus* cf. *orientalis*	0	1	0	**1**	0.60
inf sf	*Unionites canalensis*	0	1	0	**1**	0.60
inf sf	*Unionites fassaensis*	0	1	0	**1**	0.60
epi gr/dv	Gastropod ind. sp. A	0	1	0	**1**	0.60
	Richness	7	15	8	18	
	Individuals	45	105	18	168	
	Dominance D	0.18	0.16	0.29	0.16	
	mean richness **10**			mean D **0.21**		

epi - epifaunal, sinf - semi-infaunal/endobyssate, inf - infaunal, gr - grazer, dv -detritivor, sf -suspension feeder

***Protogusarella smithi* association**							
ecology	**species/sample**	**BD-B-1**	**BD-B-0**	**VR-2**	**BD-A-3**	**Sum**	**%**
epi sf	*Protogusarella smithi*	400	50	48	59	**557**	52.70
epi sf	*Piarorhynchella triassica*	100	24	31	2	**157**	14.85
epi sf	*Eumorphotis ericius*	21	9	35	31	**96**	9.08
epi sf	*Promyalina putiatinensis*	40	7	39	5	**91**	8.61
sinf sf	*Bakevellia exporrecta*	7	19	0	34	**60**	5.68
inf sf	*Sementiconcha recuperator*	0	3	1	19	**23**	2.18
sinf sf	*Bakevellia costata*	0	7	0	8	**15**	1.42
epi sf	*Leptochondria nuetzeli*	0	0	0	14	**14**	1.32
epi sf	*Eumorphotis* cf. *venetiana*	0	11	0	0	**11**	1.04
inf sf	*Unionites fassaensis*	0	3	2	4	**9**	0.85
epi gr/dv	Gastropod ind. sp. A	0	6	0	1	**7**	0.66
epi sf	*Eumorphotis* cf. *multiformis*	0	3	3	0	**6**	0.57
epi gr/dv	*Natiria* cf. *costata*	0	2	0	2	**4**	0.38
inf sf	*Neoschizodus laevigatus*	0	0	3	0	**3**	0.28
epi sf	*Eumorphotis virginensis*	0	0	1	0	**1**	0.09
epi sf	*Myalinella* sp. A	0	0	0	1	**1**	0.09
epi sf	*Pernopecten* sp. A	0	0	1	0	**1**	0.09
inf sf	*Trigonodus* cf. *sandbergi*	0	0	0	1	**1**	0.09
	Richness	5	12	10	13	18	
	Individuals	568	144	164	181	1057	
	Dominance D	0.53	0.18	0.22	0.19	0.32	

mean richness **10** mean D **0.28**

***Piarorhynchella triassica* association**					
ecology	**species/sample**	**HC-B-1**	**HC-C-1**	**Sum**	**%**
epi sf	*Piarorhynchella triassica*	20	97	**117**	88.64
epi sf	*Protogusarella smithi*	5	2	**7**	5.30
epi sf	*Eumorphotis* cf. *multiformis*	0	3	**3**	2.27
sinf sf	*Bakevellia exporrecta*	0	2	**2**	1.52
epi sf	*Eumorphotis ericius*	0	1	**1**	0.76
epi gr/dv	Gastropod ind. sp. A	0	1	**1**	0.76
s c	Ammonoid ind. sp. B	0	1	**1**	0.76
	Richness	2	7	7	
	Individuals	25	107	132	
	Dominance D	0.68	0.82	0.79	

mean richness **4.5** mean D **0.75**

epi - epifaunal, sinf - semi-infaunal/endobyssate, inf - infaunal, gr - grazer, dv -detritivor, sf -suspension feeder, s c - secondary consumer

B. Associations of the Dinwoody Formation (Chapter 3)

***Unionites fassaensis* association**

ecology	species/sample	GV-B-2	GV-A-1	GV-A-4	GV-B-1	GV-A-2	HS-1	Sum	%
inf sf	*Unionites fassaensis*	70	35	57	46	21	1	**230**	95.04
inf sf	*Unionites canalensis*	7	0	2	0	0	0	**9**	3.72
epi sf	*Promyalina spathi*	0	0	1	1	0	0	**2**	0.83
epi sf	*Claraia mulleri*	0	0	0	1	0	0	**1**	0.41
	Richness	2	1	3	3	1	1	**4**	
	Individuals	77	35	60	48	21	1	**242**	
	Dominance D	0.83	1.00	0.90	0.92	1.00	1.00	**0.905**	
				mean richness	**1.833**		mean D	**0.943**	

***Lingula borealis* association**

ecology	species/sample	HP-1	HP-3	LS-5/a	HP-13	GV-B-B	Sum	%
inf sf	*Lingula borealis*	55	50	139	48	46	**338**	95.75
epi sf	*Promyalina spathi*	0	0	4	0	0	**4**	1.13
sinf sf	*Pteria ussurica*	3	0	0	0	0	**3**	0.85
inf sf	*Unionites fassaensis*	0	0	3	0	0	**3**	0.85
epi sf	*Eumorphotis multiformis*	0	3	0	0	0	**3**	0.85
inf sf	*Unionites canalensis*	1	0	1	0	0	**2**	0.57
	Taxa/Richness	3	2	4	1	1	**6**	
	Individuals	59	53	147	48	46	**353**	
	Dominance D	0.87	0.89	0.90	1.00	1.00	**0.92**	
				mean richness	**2.2**		mean D	**0.9**	

***Leptochondria occidanea* association**

ecology	species/sample	TM-3	TM-(8/9)	TM-9	TM-2	TM-1	Sum	%
epi sf	*Leptochondria occidanea*	3	8	1	1	6	**19**	86.36
epi sf	*Periallus woodsidensis*	0	2	0	0	0	**2**	9.09
epi sf	*Eumorphotis multiformis*	1	0	0	0	0	**1**	4.55
	Taxa/Richness	2	2	1	1	1	**3**	
	Individuals	4	10	1	1	6	**22**	
	Dominance D	0.63	0.68	1.00	1.00	1.00	**0.76**	
				mean richness	**1.4**		mean D	**0.9**	

epi - epifaunal, sinf - semi-infaunal/endobyssate, inf - infaunal, gr - grazer, dv -detritivor, sf -suspension feeder

***Pteria ussurica* association**							
ecology	**species/sample**	**GV-A-8**	**GV-B-4**	**GV-A-7**	**SC-1/L**	**Sum**	**%**
sinf sf	*Pteria ussurica*	67	134	45	1	**247**	95.74
inf sf	*Unionites fassaensis*	7	1	0	0	**8**	3.10
epi sf	*Leptochondria occidanea*	0	**1**	0	0	**1**	0.39
epi sf	*Myalinella postcarbonica*	1	0	0	0	**1**	0.39
epi gr/dv	*Coelostylina* sp. A	1	0	0	0	**1**	0.39
	Taxa/Richness	4	3	1	1	**5**	
	Individuals	76	136	45	1	**258**	
	Dominance D	0.79	0.97	1.00	1.00	**0.92**	
	mean richness		**2.3**		mean D	**0.9**	

Eumorphotis multiformis association									
ecology	**species/sample**	**HP-5**	**LS-7**	**LS-5/b**	**SC-1**	**HP-2L**	**HS-L-1**	**Sum**	**%**
epi sf	*Eumorphotis multiformis*	17	72	37	3	17	4	**150**	51.02
inf sf	*Lingula borealis*	0	12	21	0	0	0	**33**	11.22
epi sf	*Eumorphotis* cf. *ericius*	0	28	3	0	0	0	**31**	10.54
epi sf	*Promyalina spathi*	0	13	12	0	2	0	**27**	9.18
inf sf	*Unionites fassaensis*	6	2	13	2	0	0	**23**	7.82
epi sf	*Eumorphotis amplicostata*	8	1	2	0	3	0	**14**	4.76
epi gr/dv	*Coelostylina* sp. A	0	12	0	0	0	0	**12**	4.08
inf sf	*Unionites canalensis*	0	0	2	0	0	0	**2**	0.68
sinf sf	*Pteria ussurica*	0	1	0	0	1	0	**2**	0.68
	Taxa/Richness	3	8	7	2	4	1	**9**	
	Individuals	31	141	90	5	23	4	**294**	
	Dominance D	0.40	0.32	0.26	0.52	0.57	1.00	**0.30**	
			mean richness		**4.2**		mean D	**0.5**	

epi - epifaunal, sinf - semi-infaunal/endobyssate, inf - infaunal, gr - grazer, dv -detritivor, sf -suspension feeder

Unionites fassaensis-Lingula borealis association					
ecology	**species/sample**	**LS-4/a**	**CM**	**Sum**	**%**
inf sf	*Unionites fassaensis*	73	17	**90**	39.65
inf sf	*Lingula borealis*	72	12	**84**	37.00
epi sf	*Leptochondria occidanea*	19	0	**19**	8.37
epi sf	*Promyalina spathi*	3	8	**11**	4.85
epi sf	*Claraia aurita*	0	10	**10**	4.41
sinf sf	*Pteria ussurica*	6	0	**6**	2.64
inf sf	*Unionites canalensis*	4	0	**4**	1.76
epi sf	*Myalinella postcarbonica*	0	3	**3**	1.32
	Taxa/Richness	6	5	**8**	
	Individuals	177	50	**227**	
	Dominance D	0.35	0.24	**0.31**	
	mean richness	**5.5**		mean D	**0.3**

Unionites fassaensis-Pteria ussurica association						
ecology	**species/sample**	**GV-A-5**	**GV-B-3**	**LPA-2**	**Sum**	**%**
inf sf	*Unionites fassaensis*	57	17	62	**136**	43.17
sinf sf	*Pteria ussurica*	43	23	29	**95**	30.16
epi gr/dv	*Dicellonema abrekensis*	0	0	38	**38**	12.06
epi sf	*Promyalina putiatinensis*	0	0	12	**12**	3.81
epi sf	*Promyalina spathi*	1	0	10	**11**	3.49
inf sf	*Unionites canalensis*	2	0	6	**8**	2.54
inf sf	*Neoschizodus laevigatus*	5	0	0	**5**	1.59
epi sf	*Claraia mulleri*	5	0	0	**5**	1.59
epi sf	*Claraia cf. stachei*	0	0	2	**2**	0.63
epi sf	*Leptochondria occidanea*	0	0	1	**1**	0.32
epi sf	*Myalinella postcarbonica*	0	0	1	**1**	0.32
epi gr/dv	*Coelostylina* sp. A	1	0	0	**1**	0.32
	Taxa/Richness	7	2	9	**12**	
	Individuals	114	40	161	**315**	
	Dominance D	0.40	0.51	0.25	**0.30**	
	mean richness	**6**		mean D	**0.4**	

epi - epifaunal, sinf - semi-infaunal/endobyssate, inf - infaunal, gr - grazer, dv -detritivor, sf -suspension feeder

C. Associations of the Thaynes Group and the Sinbad Formation (Chapter 4)

***Unionites* cf. *canalensis* association**					
ecology	**species/sample**	**DV-1**	**DV-2**	**Sum**	**%**
inf sf	*Unionites* cf. *canalensis*	16	3	**19**	42.22
epi sf	*Eumorphotis multiformis*	0	15	**15**	33.33
inf sf	*Lingularia borealis*	6	4	**10**	22.22
inf sf	*Unionites* cf. *fassaensis*	1	0	**1**	2.22
	Richness	3	3	**4**	
	Individuals	23	22	**45**	
	Dominance D	0.554	0.517	**0.339**	
	mean richness	**3**	mean D	**0.54**	

***Eumorphotis ericius* association**							
ecology	**species/sample**	**CP-3**	**CP-5**	**CP-2**	**MV-10**	**Sum**	**%**
epi sf	*Eumorphotis ericius*	27	34	16	17	**94**	68.61
epi sf	*Eumorphotis multiformis*	0	0	0	16	**16**	11.68
sinf sf	*Bakevellia* cf. *exporrecta*	9	0	0	1	**10**	7.30
epi sf	*Leptochondria occidanea*	1	0	0	7	**8**	5.84
inf sf	*Unionites* cf. *canalensis*	8	0	0	0	**8**	5.84
sinf sf	*Permophorus* cf. *bregeri*	0	0	0	1	**1**	0.73
	Richness	4	1	1	5	**6**	
	Individuals	45	34	16	42	**137**	
	Dominance D	0.432	1	1	0.338	**0.497**	
	mean richness	**2.75**	mean D	**0.69**			

***Leptochondria occidanea* association**								
ecology	**species/sample**	**CP-1**	**CP-7**	**CP-8**	**DH-1-3**	**TO-A-5**	**Sum**	**%**
epi sf	*Leptochondria occidanea*	13	13	26	103	37	**192**	86.10
epi sf	*Confusionella loczyi*	0	0	0	21	0	**21**	9.42
inf sf	*Neoschizodus laevigatus*	0	0	0	3	0	**3**	1.35
inf sf	*Lingularia borealis*	0	0	0	0	2	**2**	0.90
epi gr/dv	*Chartronella* ? sp. A	0	0	0	0	2	**2**	0.90
epi gr/dv	*Worthenia windowblindensis*	0	0	0	1	0	**1**	0.45
free epi	*Pernopecten* sp. A	0	0	0	0	1	**1**	0.45
inf sf	*Sementiconcha recuperator*	0	0	0	1	0	**1**	0.45
	Richness	1	1	1	5	4	**8**	
	Individuals	13	13	26	129	42	**223**	
	Dominance D	1	1	1	0.665	0.781	**0.751**	
	mean richness	**2.4**	mean D	**0.88**				

epi - epifaunal, sinf - semi-infaunal/endobyssate, inf - infaunal, gr - grazer, dv -detritivor, sf -suspension feeder

***Promysidialla* sp. A association**											
ecology	**species/sample**	**SR-1**	**SR-2**	**SR-3**	**SR-4**	**SR-5**	**MV-2**	**TO-A-6**	**TO-A-1**	**Sum**	**%**
epi sf	*Promysidiella* sp. A	28	129	57	58	9	0	29	39	**349**	54.79
epi gr/dv	*Abrekopsis* cf. *depressispirus*	0	33	19	1	13	45	0	1	**112**	17.58
epi sf	*Leptochondria occidanea*	0	12	5	0	0	0	21	15	**53**	8.32
epi sf	*Confusionella loczyi*	5	2	0	0	0	0	0	17	**24**	3.77
epi gr/dv	*Polygyrina* sp. A	0	1	6	0	0	12	0	3	**22**	3.45
sinf sf	*Permophorus* cf. *bregeri*	0	0	0	17	2	0	0	0	**19**	2.98
epi gr/dv	*Chartronella*? sp. A	2	6	0	1	0	0	0	3	**12**	1.88
epi sf	*Leptochondria xijinwulanensis*	0	0	2	0	0	0	0	7	**9**	1.41
inf sf	*Neoschizodus laevigatus*	0	0	0	1	0	0	7	0	**8**	1.26
sinf sf	*Bakevellia* cf. *exporrecta*	0	1	0	1	0	0	5	1	**8**	1.26
inf sf	*Unionites* cf. *canalensis*	0	0	0	1	0	0	0	5	**6**	0.94
inf chem.	*Sinbadiella pygmaea*	0	3	0	0	0	0	0	2	**5**	0.78
epi sf	*Crittendenia?* sp. A	2	1	1	0	0	0	0	0	**4**	0.63
inf sf	*Unionites* cf. *fassaensis*	0	2	0	0	0	0	0	1	**3**	0.47
epi sf	*Eumorphotis multiformis*	1	0	0	0	0	0	0	0	**1**	0.16
inf sf	*Sementiconcha recuperator*	0	0	0	1	0	0	0	0	**1**	0.16
epi gr/dv	*Neritaria costata*	0	0	0	1	0	0	0	0	**1**	0.16
	Richness	5	10	6	8	3	2	4	11	**17**	
	Individuals	38	190	90	81	24	57	62	94	**636**	
	Dominance D	0.57	0.5	0.45	0.56	0.44	0.67	0.35	0.24	**0.34**	
	mean richness	**6.1**	mean D	**0.5**							

***Confusionella loczyi* association**											
	species/sample	**TO-A-2**	**DH-1-0**	**DH-1-2**	**DH-1-0a**	**DH-1-12**	**DH-1-9**	**DH-1-5**	**TO-A-3**	**Sum**	**%**
epi sf	*Leptochondria occidanea*	8	22	11	34	132	109	94	9	**419**	82.48
epi sf	*Confusionella loczyi*	9	10	9	1	14	9	0	2	**54**	10.63
inf sf	*Neoschizodus laevigatus*	13	1	0	0	0	0	0	0	**14**	2.76
inf sf	*Lingularia borealis*	1	0	0	0	0	1	2	2	**6**	1.18
epi gr/dv	*Chartronella*? sp. A	0	5	0	0	0	0	0	0	**5**	0.98
epi gr/dv	*Worthenia windowblindensis*	2	0	0	0	0	2	0	0	**4**	0.79
free epi	*Pernopecten* sp. A	0	1	1	0	0	0	1	0	**3**	0.59
inf sf	*Sementiconcha recuperator*	1	0	0	0	0	0	0	1	**2**	0.39
inf chem.	*Sinbadiella pygmaea*	0	0	0	0	0	1	0	0	**1**	0.20
	Richness	6	5	3	2	2	5	3	4	**9**	
	Individuals	34	39	21	35	146	122	97	14	**508**	
	Dominance D	0.28	0.4	0.46	0.94	0.83	0.8	0.94	0.46	**0.693**	
	mean richness	**3.8**	mean D	**0.6**							

epi - epifaunal, sinf - semi-infaunal/endobyssate, inf - infaunal, gr - grazer, dv -detritivor, sf -suspension feeder, chem. -chemosymbiont

***Bakevellia* cf. *exporrecta* association**												
ecology	**species/sample**	**DH-3-2**	**MV-4**	**MV-3**	**CP-0**	**CP-101**	**MV-12**	**MV-7**	**MV-9**	**CP-4**	**Sum**	**%**
sinf sf	*Bakevellia* cf. *exporrecta*	69	9	10	57	4	17	9	28	37	**240**	86.02
epi sf	*Eumorphotis ericius*	0	0	0	0	4	0	0	0	12	**16**	5.73
epi sf	*Leptochondria occidanea*	0	3	2	0	0	0	0	0	0	**5**	1.79
epi sf	*Promysidiella* sp. A	0	0	0	0	3	0	2	0	0	**5**	1.79
inf sf	*Unionites* cf. *fassaensis*	0	1	4	0	0	0	0	0	0	**5**	1.79
inf sf	*Neoschizodus laevigatus*	0	0	0	0	0	5	0	0	0	**5**	1.79
epi sf	*Eumorphotis multiformis*	0	0	1	0	0	0	0	0	0	**1**	0.36
epi sf	*Eumorphotis hinnitidea*	0	0	0	0	0	0	0	0	1	**1**	0.36
sinf sf	*Permophorus* cf. *bregeri*	0	0	1	0	0	0	0	0	0	**1**	0.36
	Richness	1	3	5	1	3	2	2	1	3	**9**	
	Individuals	69	13	18	57	11	22	11	28	50	**279**	
	Dominance D	1	0.5	0.4	1	0.3	0.6	0.7	1	0.61	**0.74**	
	mean richness	**2.3**	mean D	**0.7**								

***Strobeus batteni* association**					
ecology	**species/sample**	**gs2**	**gs1**	**Sum**	**%**
epi cv	*Strobeus batteni*	22	29	**51**	45.54
epi gr/dv	*Laubopsis*? sp. A	31	11	**42**	37.50
epi sf	*Confusionella loczyi*	6	7	**13**	11.61
epi sf	*Leptochondria occidanea*	0	3	**3**	2.68
epi gr/dv	*Polygyrina* sp. A	2	0	**2**	1.79
inf sf	*Unicardium* sp. A	1	0	**1**	0.89
	Richness	5	4	**6**	
	Individuals	62	50	**112**	
	Dominance D	0.387	0.408	**0.363**	
	mean richness	**4.5**	mean D	**0.4**	

epi - epifaunal, sinf - semi-infaunal/endobyssate, inf - infaunal, gr - grazer, dv -detritivor, sf -suspension feeder

D. Associations of the Werfen Formation (Chapter 5)

***Unionites fassaensis* association**											
ecology	**species/sample**	**AG-1**	**AG-2**	**AG-3**	**AG-4**	**RG-1**	**RG-2**	**RG-3**	**RG-4**	**Sum**	**%**
inf sf	*Unionites fassaensis*	15	37	205	25	1	7	1	120	**411**	85.09
sinf sf	*Pteria* cf. *ussurica*	4	11	1	0	0	1	0	0	**17**	3.52
epi gr/dv	*Coelostylina werfensis*	2	4	2	0	0	6	3	0	**17**	3.52
epi gr/dv	Bellerophontid sp. A	1	15	0	0	0	0	0	0	**16**	3.31
inf sf	*Lingula tenuissima*	3	2	3	0	0	0	0	1	**9**	1.86
epi sf	*Claraia aurita*	0	0	0	3	0	0	0	0	**3**	0.62
epi sf	*Eumorphotis multiformis*	0	0	1	0	1	0	1	0	**3**	0.62
epi sf	*Eumorphotis* sp. A	0	2	0	0	0	0	0	0	**2**	0.41
inf sf	*Neoschizodus orbicularis*	0	2	0	0	0	0	0	0	**2**	0.41
inf sf	*Neoschizodus laevigatus*	0	0	0	0	0	0	2	0	**2**	0.41
	Richness	5	7	5	2	3	3	4	2	**10**	
	Individuals	25	73	212	28	3	14	7	121	**483**	
	Dominance D	0.408	0.327	0.935	0.809	0.333	0.439	0.306	0.984	**0.73**	
	mean richness	**3.88**		mean D	**0.57**						

***Neoschizodus orbicularis* association**					
ecology	**species/sample**	**AG-12**	**AG-9**	**Sum**	**%**
inf sf	*Neoschizodus orbicularis*	143	121	**264**	58.93
epi sf	*Claraia aurita*	44	12	**56**	12.50
inf sf	*Neoschizodus laevigatus*	22	23	**45**	10.04
inf sf	*Lingula tenuissima*	2	34	**36**	8.04
epi gr/dv	*Coelostylina werfensis*	21	0	**21**	4.69
inf sf	*Unionites fassaensis*	1	15	**16**	3.57
epi sf	*Towapteria scythica*	0	9	**9**	2.01
epi sf	*Eumorphotis multiformis*	0	1	**1**	0.22
	Richness	6	7	**8**	
	Individuals	233	215	**448**	
	Dominance D	0.43	0.363	**0.38**	
	mean richness	**6.5**	mean D	**0.4**	

epi - epifaunal, sinf - semi-infaunal/endobyssate, inf - infaunal, gr - grazer, dv -detritivor, sf -suspension feeder

Claraia aurita association												
ecology	**species/sample**	**RG-8**	**RG-9**	**AG-5**	**AG-7**	**AG-8**	**AG-13**	**RG-5**	**RG-6**	**RG-7**	**Sum**	**%**
epi sf	*Claraia aurita*	15	60	17	122	92	4	8	95	1	**414**	85.89
epi sf	*Towapteria scythica*	0	0	0	0	25	0	0	1	0	**26**	5.39
epi gr/dv	*Coelostylina werfensis*	0	0	3	1	0	0	5	0	1	**10**	2.07
inf sf	*Unionites fassaensis*	0	0	2	1	5	0	0	0	0	**8**	1.66
epi gr/dv	Bellerophontid sp. A	0	0	5	0	1	0	0	0	0	**6**	1.24
inf sf	*Unionites canalensis*	0	0	0	0	0	0	5	0	0	**5**	1.04
inf sf	*Neoschizodus orbicularis*	0	0	0	0	4	0	0	0	0	**4**	0.83
inf sf	*Lingula tenuissima*	0	0	0	0	1	1	0	2	0	**4**	0.83
sinf sf	*Pteria* cf. *ussurica*	0	0	0	0	2	0	0	0	0	**2**	0.41
epi sf	*Eumorphotis multiformis*	0	1	0	0	1	0	0	0	0	**2**	0.41
inf sf	*Neoschizodus laevigatus*	0	0	0	0	1	0	0	0	0	**1**	0.21
	Richness	1	2	4	3	9	2	3	3	2	**11**	
	Individuals	15	61	27	124	132	5	18	98	2	**482**	
	Dominance D	1	0.968	0.449	0.968	0.524	0.68	0.352	0.94	0.5	**0.74**	
	mean richness	**3.22**		mean D	**0.71**							

Claraia clarai association									
ecology	**species/sample**	**AG-14**	**AG-15**	**AG-17**	**RG-12**	**RG-15**	**RG-11**	**Sum**	**%**
epi sf	*Claraia clarai*	18	13	42	25	2	1	**101**	59.06
inf sf	*Neoschizodus laevigatus*	0	36	0	0	0	0	**36**	21.05
inf sf	*Unionites canalensis*	0	9	4	4	1	0	**18**	10.53
inf sf	*Neoschizodus orbicularis*	0	3	5	0	0	0	**8**	4.68
epi sf	*Eumorphotis* sp. A	0	0	4	0	0	0	**4**	2.34
epi sf	*Eumorphotis multiformis*	1	1	0	0	0	0	**2**	1.17
epi sf	*Claraia aurita*	0	0	0	0	0	1	**1**	0.58
inf sf	*Unionites fassaensis*	1	0	0	0	0	0	**1**	0.58
	Richness	3	5	4	2	2	2	**8**	
	Individuals	20	62	55	29	3	2	**171**	
	Dominance D	0.815	0.405	0.602	0.762	0.556	0.5	**0.41**	
	mean richness	**3**		mean D	**0.61**				

epi - epifaunal, sinf - semi-infaunal/endobyssate, inf - infaunal, gr - grazer, dv -detritivor, sf -suspension feeder

***Pseudomurchisonia kokeni* assocation**						
ecology	**species/sample**	**AG-28**	**AG-29**	**RG-25**	**Sum**	**%**
epi gr/dv	*Pseudomurchisonia kokeni*	60	120	35	**215**	73.88
epi sf	*Claraia aurita*	0	41	5	**46**	15.81
inf sf	*Unionites canalensis*	0	14	2	**16**	5.50
inf sf	*Neoschizodus elongatus*	0	11	0	**11**	3.78
inf sf	*Stutchburia* sp. A	0	0	2	**2**	0.69
epi sf	*Eumorphotis multiformis*	0	0	1	**1**	0.34
	Richness	1	4	5	**6**	
	Individuals	60	186	45	**291**	
	Dominance D	1	0.474	0.622	**0.58**	
	mean richness	**3,33**	mean D		**0,7**	

***Neoschizodus orbicularis-Unionites fassaensis* association**							
ecology	**species/sample**	**LOP-1**	**RG-19**	**AG-25**	**AG-26**	**Sum**	**%**
inf sf	*Neoschizodus orbicularis*	76	16	0	2	**94**	53.41
inf sf	*Unionites fassaensis*	15	10	0	0	**25**	14.20
inf sf	*Neoschizodus elongatus*	0	19	5	0	**24**	13.64
epi sf	*Claraia aurita*	8	4	1	2	**15**	8.52
inf sf	*Neoschizodus laevigatus*	9	0	0	0	**9**	5.11
sinf sf	*Pteria* cf. *ussurica*	0	6	0	0	**6**	3.41
inf sf	*Unionites canalensis*	0	0	2	0	**2**	1.14
inf sf	*Stutchburia* sp. A	0	1	0	0	**1**	0.57
	Richness	4	6	3	2	**8**	
	Individuals	108	56	8	4	**176**	
	Dominance D	0.527	0.246	0.469	0.5	**0.34**	
	mean richness	**3.75**	mean D		**0.44**		

epi - epifaunal, sinf - semi-infaunal/endobyssate, inf - infaunal, gr - grazer, dv -detritivor, sf -suspension feeder

***Unionites fassaensis-Claraia aurita* association**																			
ecology	**species/sample**	**LOP-2**	**AG-31**	**RG-13**	**RG-14**	**AG-19**	**AG-23**	**AG-27**	**RG-23**	**RG-16**	**RG-17**	**RG-18**	**RG-40**	**AG-32**	**RG-22**	**RG-24**	**AG-30**	**Sum**	**%**
inf sf	*Unionites canalensis*	24	15	12	3	35	12	8	2	5	6	12	31	0	1	3	1	**170**	37.36
epi sf	*Claraia aurita*	3	5	2	1	6	7	25	7	2	5	3	64	8	0	5	2	**145**	31.87
inf sf	*Unionites fassaensis*	20	0	0	3	0	0	0	0	11	3	0	15	0	1	0	0	**53**	11.65
inf sf	*Neoschizodus orbicularis*	0	0	8	1	9	1	2	0	0	9	0	0	0	0	0	0	**30**	6.59
epi sf	*Claraia clarai*	0	0	4	3	2	0	0	0	7	4	0	0	0	1	0	0	**21**	4.62
epi gr/dv	*Coelostylina werfensis*	0	4	0	1	6	0	0	0	0	0	0	0	1	0	0	0	**12**	2.64
sinf sf	*Pteria* cf. *ussurica*	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	**9**	1.98
epi sf	*Eumorphotis multiformis*	0	0	0	0	0	5	0	0	0	1	0	0	0	1	0	0	**7**	1.54
inf sf	*Neoschizodus laevigatus*	0	0	3	0	0	0	0	0	0	2	0	0	0	0	0	0	**5**	1.10
inf sf	*Neoschizodus elongatus*	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	**2**	0.44
epi sf	*Eumorphotis* cf. *hinnitidea*	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0.22
	Richness	3	3	6	6	5	4	3	3	4	7	2	4	2	4	2	2	**11**	
	Individuals	47	24	30	12	58	25	35	11	25	30	15	119	9	4	8	3	**455**	
	Dominance D	0.4	0.5	0.3	0.2	0.4	0.4	0.6	0.5	0.3	0.2	0.7	0.4	0.8	0.3	0.5	0.6	**0.26**	
	mean richness	**3.8**	mean D	**0.4**															

***Coelostylina werfensis* association**													
ecology	**species/sample**	**AG-18**	**AG-20**	**AG-22**	**RG-41**	**RG-41a**	**RG-42**	**RG-43**	**RG-20**	**RG-21**	**AG-34**	**Sum**	**%**
epi gr/dv	*Coelostylina werfensis*	17	23	69	19	37	15	39	30	25	1	**275**	63.36
epi sf	*Claraia aurita*	3	0	7	7	3	14	9	7	3	0	**53**	12.21
epi sf	*Claraia clarai*	4	0	25	0	0	0	0	0	4	0	**33**	7.60
inf sf	*Unionites canalensis*	7	1	0	5	2	6	2	3	4	1	**31**	7.14
inf sf	*Unionites fassaensis*	2	1	1	18	0	5	0	0	1	0	**28**	6.45
sinf sf	*Pteria* cf. *ussurica*	0	0	4	0	0	0	0	0	0	0	**4**	0.92
inf sf	*Neoschizodus orbicularis*	3	0	1	0	0	0	0	0	0	0	**4**	0.92
inf sf	*Neoschizodus elongatus*	0	0	0	0	0	3	0	1	0	0	**4**	0.92
epi sf	*Eumorphotis multiformis*	0	0	0	0	0	0	0	1	0	0	**1**	0.23
epi gr/dv	Bellerophontid sp. A	0	0	0	0	0	0	0	1	0	0	**1**	0.23
	Richness	6	3	6	4	3	5	3	6	5	2	**10**	
	Individuals	36	25	107	49	42	43	50	43	37	2	**434**	
	Dominance D	0.29	0.85	0.48	0.32	0.78	0.27	0.64	0.52	0.49	0.5	**0.43**	
	mean richness	**4.3**	mean D	**0.51**									

epi - epifaunal, sinf - semi-infaunal/endobyssate, inf - infaunal, gr - grazer, dv -detritivor, sf -suspension feeder

Bulk assocation Campil Member

ecology	species/sample	RG-L2	RG-44	RG-45	LOP-3	LOP-4	LOP-5	LOP-6	LOP-7	LOP-L	CB-1	CB-2	CB-3	CB-4	CB-5	CB-7	Sum	%
inf sf	*Unionites fassaensis*	12	21	9	3	27	21	9	87	0	7	9	0	5	1	9	**220**	69.62
inf sf	*Neoschizodus laevigatus*	0	0	0	0	13	4	18	0	0	0	0	0	0	0	0	**35**	11.08
fr epi sf	*Scythentolium* sp. A	0	0	0	0	0	0	0	0	0	0	0	24	9	0	0	**33**	10.44
inf sf	*Unionites canalensis*	0	1	3	9	2	0	0	0	6	0	0	0	0	0	0	**21**	6.65
epi sf	*Eumorphotis multiformis*	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	**3**	0.95
sinf sf	*Bakevellia exporrecta*	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	**3**	0.95
epi sf	*Eumorphotis* cf. *beneckei*	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	**1**	0.32
	Richness	1	2	2	3	3	2	2	2	1	1	2	1	2	2	1	**7**	
	Individuals	12	22	12	15	42	25	27	88	6	7	10	24	14	3	9	**316**	
	Dominance D	1	0.91	0.63	0.44	0.51	0.73	0.56	0.98	1	1	0.82	1	0.54	0.6	1	**0.51**	

mean richness **1.8** mean D **0.78**

***Bakevellia exporrecta* association**

ecology	species/sample	WH-8	WH-9	CB-18	CB-19	VV-2	WH-10	Sum	%
sinf sf	*Bakevellia exporrecta*	12	2	8	27	52	24	**125**	45.13
epi gr/dv	*Natiria costata*	10	0	0	0	34	14	**58**	20.94
inf sf	*Neoschizodus laevigatus*	3	0	0	2	8	16	**29**	10.47
epi sf	*Eumorphotis telleri*	1	2	0	0	9	8	**20**	7.22
epi sf	*Leptochondria albertii*	0	0	0	0	0	13	**13**	4.69
epi gr/dv	*Werfenella rectecostata*	1	2	0	0	0	8	**11**	3.97
sinf sf	*Bakevellia albertii*	1	0	0	0	3	5	**9**	3.25
epi sf	*Eumorphotis* cf. *hinnitidea*	3	0	0	0	0	0	**3**	1.08
inf sf	*Unionites canalensis*	0	0	0	0	3	0	**3**	1.08
epi sf	*Costatoria subrotunda*	0	0	0	0	2	0	**2**	0.72
epi sf	*Eumorphotis multiformis*	0	0	1	0	0	0	**1**	0.36
inf sf	*Unionites fassaensis*	0	0	1	0	0	0	**1**	0.36
epi c	*Praeaplocoma hessi*	0	0	0	0	0	1	**1**	0.36
epi gr/dv	*Worthenia* sp. A	0	0	0	0	1	0	**1**	0.36
	Richness	7	3	3	2	8	8	**14**	
	Individuals	31	6	10	29	112	89	**277**	
	Dominance D	0.28	0.33	0.66	0.87	0.32	0.17	**0.27**	

mean richness **5.17** mean D **0.44**

epi - epifaunal, sinf - semi-infaunal/endobyssate, inf - infaunal, gr - grazer, dv -detritivor, sf -suspension feeder, c - carnivore

Natiria costata association												
ecology	**species/sample**	**CB-14**	**CB-10**	**LOP-8**	**CB-13**	**WH-7**	**CB-9**	**VV-1**	**CB-16**	**CB-17**	**Sum**	**%**
sinf sf	*Bakevellia exporrecta*	1	0	1	0	0	1	7	0	0	**10**	6.90
epi gr/dv	*Natiria costata*	3	4	12	8	31	5	25	8	7	**103**	71.03
inf sf	*Neoschizodus laevigatus*	8	6	0	0	0	1	3	3	2	**23**	15.86
inf sf	*Unionites fassaensis*	0	3	0	0	0	1	0	0	0	**4**	2.76
epi sf	*Eumorphotis telleri*	0	0	1	0	0	0	0	1	0	**2**	1.38
epi gr/dv	*Werfenella rectecostata*	0	0	0	0	2	0	0	0	0	**2**	1.38
epi sf	*Eumorphotis* cf. *hinnitidea*	0	0	0	0	1	0	0	0	0	**1**	0.69
	Richness	3	3	3	1	3	4	3	3	2	**7**	
	Individuals	12	13	14	8	34	8	35	12	9	**145**	
	Dominance D	0.51	0.36	0.74	1	0.84	0.44	0.56	0.51	0.65	**0.54**	
	mean richness	**2.78**	mean D	**0.62**								

epi - epifaunal, sinf - semi-infaunal/endobyssate, inf - infaunal, gr - grazer, dv -detritivor, sf -suspension feeder

Curriculum vitae

Name	Richard
Last name	Hofmann
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Place of birth	Zeitz, Germany
Nationality	German

Education

03/2009 – 11/2013
PhD-Student, Palaeontological Institute and Museum, Zurich University
Thesis: "Early Triassic recovery from the end-Permian mass extinction of benthic ecosystems in the palaeotropics", advisor: Dr. Michael Hautmann, Prof. Dr. Hugo Bucher (Zurich University)

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Scientific staff Mineral Exhibition "Terra Mineralia", Freiberg

10/2002 – 12/2008
Studies in Geology/Palaeontology TU Bergakademie Freiberg, Germany
Examinations in Palaeontology, Sedimentology, and Geochemistry
Thesis "Trace fossil analysis and sedimentary environments of the "middle" Cambrian Hanneh Member, Southern Dead Sea (Burj Formation, Jordan)", advisor: Dr. Olaf Elicki (TU Bergakademie Freiberg), Dr. M. Gabriela Mángano (University of Saskatchewan).

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